THE

FUNCTIONS OF THE BRAIN

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TO

DR HUGHLINGS JACKSON

WHO FROM A CLINICAL AND PATHOLOGICAL STANDPOINT
ANTICIPATED MANY OF THE MORE IMPORTANT RESULTS OF RECENT
EXPERIMENTAL INVESTIGATION INTO THE FUNCTIONS
OF THE CEREBRAL HEMISPHERES

This Work is Dedicated

AS A MARK OF THE AUTHOR'S ESTEEM AND ADMIRATION

PREFACE.

My chief object in this book has been to present to the student of physiology or psychology a systematic exposition of the bearing of my own experiments on the functions of the brain. To do this satisfactorily I have thought it necessary to consider the functions of the cerebro-spinal system in general, with the view more especially of pointing out the mutual relations between the higher and the lower nerve centres. Throughout I have aimed at a concise digest rather than an encyclopædic account of the various researches by which our knowledge of the brain and spinal cord have been built up.

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INTRODUCTORY.

There is, perhaps, no subject in physiology of greater importance and general interest than the functions of the brain, and there are few which present to experimental investigation conditions of greater intricacy and complexity. No one who has attentively studied the results of the labours of the numerous investigators in this field of research, can help being struck by the want of harmony, and even positive contradictions, among the conclusions which apparently the same experiments and the same facts have led to in different hands. And when the seemingly well-established facts of experimentation on the brains of the lower animals are compared with those of clinical observation and morbid anatomy in man, the discord between them is frequently so great as to lead many to the opinion that physiological investigation on the lower animals is little calculated to throw true light on the functions of the human brain. These discrepancies appear less unaccountable, when the methods of experimentation and the subjects of experiment are taken into consideration. Up to quite a recent date, the principal method pursued by investigators into the functions of the brain, consisted in observing the results following the destruction, by various means, of different parts of the encephalon.

The serious nature of the operations necessary to expose the brain for purposes of experiment, and the fact that the various parts of the encephalon, though anatomically distinct, are yet so intimately combined and related to each other as to form a complex whole, make it natural to suppose that the establishment of lesions of greater or less extent in any one part, should produce such general perturbation of the functions of the organ as a whole, as to render it at least highly difficult to trace any uncomplicated connection between the symptoms produced and the lesion as such. Moreover, the degree of evolution of the central nervous system, from the simplest reflex mechanism up to the highest encephalic centres, and the differences as regards the relative independence or subordination of the lower to the higher centres, according as we ascend or descend the animal scale, introduce other complications, and render the application of the results of experiment on the brain of a frog, or a pigeon, or a rabbit, without due qualification, to the physiology of the human brain, very questionable; or even lead to conclusions seriously at variance with well-established facts of clinical and pathological observation. Notwithstanding these difficulties and discrepancies, many of which will be found, on careful examination, to be more apparent than real, experiments on animals, under conditions selected and varied at the will of the experimenter, are alone capable of furnishing precise data for sound inductions as to the functions of the brain and its various parts; the experiments performed for us by nature, in the form of diseased conditions, being rarely limited, or free from such complications as render analysis and the discovery of cause and effect extremely difficult, and in many cases practically impossible. The discovery of new methods of investigation opens up new fields of inquiry, and leads to the discovery of new truths. The discovery of the electric excitability of the brain by Fritsch and Hitzig has given a fresh impetus to researches on the functions of the brain, and thrown a new light on many obscure points in cerebral physiology and pathology. Much, however, still remains to be done. We are still only on the threshold of the inquiry, and it may be questioned whether the time has even yet arrived for an attempt to explain the mechanism of the brain and its functions. To thoughtful minds the time may seem as far off as ever; yet it is sometimes useful to review and systematise the knowledge we have so far acquired, if for no other reason than to show how much still remains to be conquered.

STRUCTURE

OF THE

BRAIN AND SPINAL CORD.

CHAPTER I.

SKETCH OF THE STRUCTURE OF THE BRAIN AND SPINAL CORD.

§ 1. The following sketch of the general structural arrangement of the cerebro-spinal system is intended mainly as a guide to the details of experimental investigation. Anatomical investigation and physiological experimentation are complementary to each other, and the combination of the two methods is especially necessary towards the elucidation of the complex functions of the brain and spinal cord. In respect to the latter, the anatomical researches of Lockhart-Clarke and others, combined with the physiological researches of Brown-Sequard, Schiff, etc., have rendered our knowledge more precise than that which we possess respecting the brain itself. The anatomical investigation of the brain is a much more difficult subject of inquiry than that of the spinal cord, and though of recent years, and particularly by Meynert, the structure of the brain has been elaborately investigated, yet the difficulties of tracing connections, and ascertaining the relations of one part to another, are so great, that the results must be accepted with extreme caution, or remain doubtful, unless substantiated by facts of physiology or pathology. I shall restrict myself, therefore, to what seems fairly well established, without entering into minute or critical detail.

§ 2. The brain is brought into relation with the periphery by thirty-one pairs of spinal and twelve cranial nerves. These nerves, or cords of communication, are separable into two great divisions, according to the nature of the function they perform. One set carry impressions from the periphery to the cord and brain, and are therefore called *afferent* nerves; while the other set carry impulses from the brain and cord to the periphery, and are therefore called *efferent* nerves. The most prominent functions performed by these nerves being the conveyance of sensory impressions and motor stimuli respectively, the restricted terms *sensory* and *motor* are frequently employed in lieu of the wider terms afferent and efferent.

The spinal nerves are connected to the spinal cord by two roots (fig. 1), one of which, the efferent or motor (5), arises from the anterior aspect of the cord; the other, the afferent or sensory (6, fig. 1), is connected with the posterior surface. After a short independent course, and the development of a ganglion (6′, fig. 1) on the posterior root, the two unite to form one trunk (7, fig. 1), which is, therefore, a mixed nerve, containing both afferent and efferent fibres. The nerve

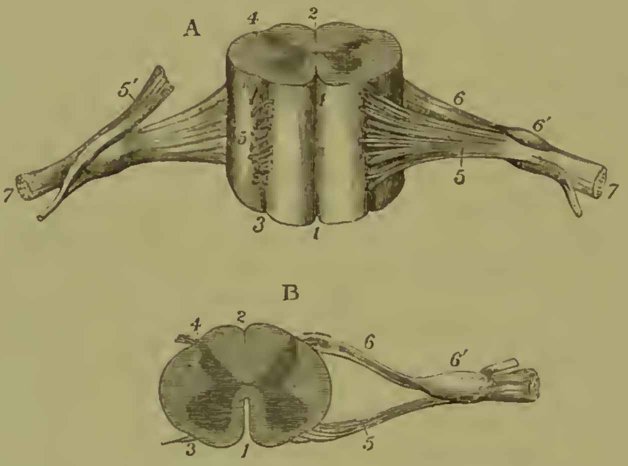


FIG. 1.—Spinal Cord (Quain). In A the anterior surface of the cord is shown, the anterior nerve root being divided on the right. In B a transverse section of the cord is exhibited, showing the crescentic shape of the grey matter in the interior. 1. The anterior median fissure. 2. Posterior median fissure. 3. Anterior lateral depression over which the anterior nerve roots are seen to spread. 4. Posterior lateral groove into which the posterior roots are seen to sink.

The anterior column is included between 1 and 3; the lateral column between 3 and 4; and the posterior column between 4 and 2.

5. The anterior root. 5′ in A = the anterior root divided. 6. The posterior roots, the fibres of which pass into the ganglion 6′. 7. The united or compound nerve.

distributes itself by minute ramifications in the receptive and active organs at the periphery, each filament remaining distinct in its whole course.

The spinal cord itself consists of central grey matter and white conducting columns or strands. The grey matter has the form of a double crescent, with the convex surfaces joined by commissures (7, 8, fig. 2), in the centre of which the central canal of the spinal cord is seen (9), and the horns of the crescents are connected respectively with the anterior and posterior roots of the spinal nerves.

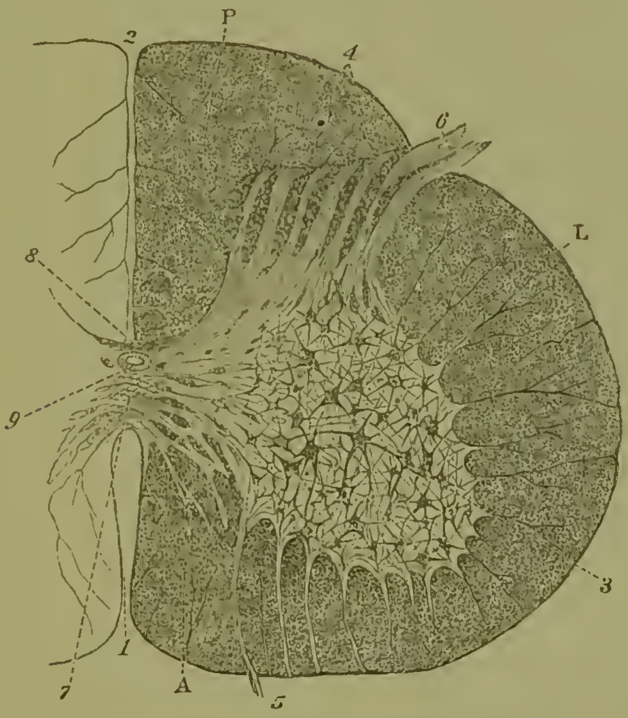


FIG. 2.—Section of Spinal Cord in the Lumbar Region, magnified.—A. The anterior column. L. The lateral column. P. The posterior column. 1. The anterior fissure. 2. The posterior fissure. 3. The anterior cornu with multipolar cells. 4. The posterior cornu, the letters placed on the *substantia gelatinosa*. 5. The anterior roots of the spinal nerve. 6. The posterior roots. 7. The anterior commissure. 8. The posterior commissure. 9. The central canal of the spinal cord lined with epithelium.

The cells of the anterior cornu are large and multipolar (3), those of the posterior small, and mingled with what is termed the gelatinous substance (4). The conducting strands form three great divisions or columns, the anterior, the lateral and posterior. (See description of figs. 1 and 2.)

§ 3. The path of efferent or motor impulses passes down the cord chiefly on the same side as that from which the motor roots emerge. Hence a hemisection of the cord causes paralysis of motion, chiefly on the same side of the body, in the parts below the section.

The sensory or afferent impressions are conveyed up to the brain chiefly in the opposite half of the cord to that into which the sensory root sinks. Hence a hemisection of the spinal cord produces diminution of sensation on the opposite side of the body in all parts below the section, and curiously at the same time exalted sensibility on the same side as the lesion.

As regards the exact localisation of the sensory and motor tracts of the spinal cord there is still some discrepancy of opinion. The antero-lateral columns of the cord are usually regarded as the chief motor paths, but the recent and careful experiments of Ludwig and Woroschiloff ('Der Verlauf der Motorischen und Sensibilen Bahnen durch das Lendenmark des Kaninchens,' 1874) place the motor paths in the lateral columns only. The anterior columns are regarded more as commissural connections between the motor nerves and adjacent segments, and not at least the direct paths of motor impulses proceeding from the brain.

The chief differences of opinion are as regards the exact localisation of the sensory tracts.

The central grey matter of the cord is regarded by Schiff, Vulpian, etc., as capable, in the absence of all other parts of the cord, of conveying sensory impressions, these being still transmitted if the grey matter is not absolutely and entirely interrupted in any part.

Schiff would distinguish between the paths of tactile impressions and those of painful sensory impressions. The former he places with Sanders-Ezn in the posterior columns, the latter in the central grey matter. Ludwig and Woroschiloff place the sensory with the motor in the lateral columns, a differentiation of the two not being anatomically possible. The posterior columns, like the anterior, become only commissural connections between the sensory roots and adjacent segments, and do not constitute the long or direct sensory paths to the brain. Their researches also confirm what other experimenters have found, viz.: that even after destruction of large areas of the lateral columns neither motion nor sensation is absolutely paralysed in any particular part; whence it is argued that a vicarious interchange of function potentially exists between different parts of the cord. Though the main results of section of different parts of the cord agree, many more observations and experiments will have to be made before it can be said that the sensory and motor paths have been exactly defined, and all views reconciled.

§ 4. After reaching the foramen magnum of the skull, the spinal cord expands into the *medulla oblongata*. Here the central canal opens out into the fourth ventricle (fig. 3). The sensory and motor tracts become dislocated, as it were, from their former position by the opening up of the spinal canal, and by the development of accessory ganglia and cerebellar connecting strands.

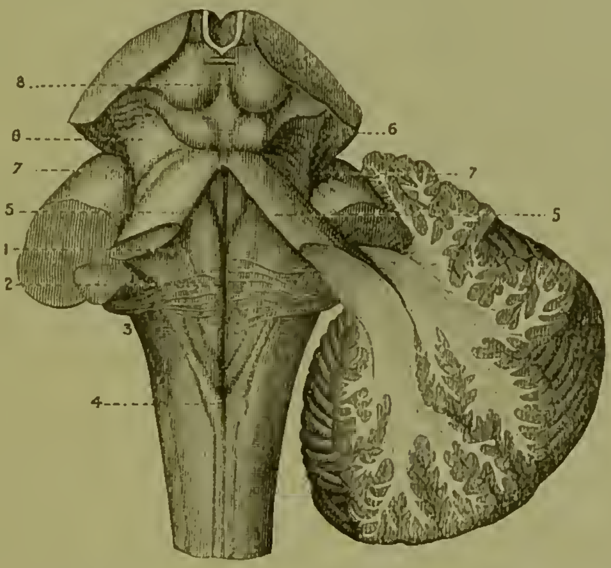


FIG. 3.—The Fourth Ventricle exposed by Division of the Cerebellum (Sappey).—On the left side the cerebellar peduncles have been cut short; on the right the middle peduncle has been cut short, while the superior and inferior retain their connections. 1. Median groove of the med. obl. bounded on each side by the *fasciculi teretes.* 2. Roots of the auditory nerve. 3. Inferior cerebellar peduncle or restiform body. 4. Posterior pyramid. 5. Superior cerebellar peduncle, or processus a cerebello ad cerebrum. 6. Fillet. 7. Crura cerebri. 8. Corpora quadrigemina.

Owing to this it is more difficult to trace the individual tracts of the spinal cord on their way upwards to the brain. Disregarding for the time the complexities arising from the development of new centres and cerebellar connections, we may follow the great sensory and motor paths. The motor paths undergo decussation at the anterior aspect of the lower extremity of the medulla oblongata, at a point termed the *decussation of the pyramids* (*d*, fig. 4).

At this point, therefore, the path of motor or efferent impulses from the hemisphere crosses to the opposite side of the cord. The decussation appears to be complete in man, but in the lower animals, such as the dog, it would seem, from the researches of Philipeaux and Vulpian, to be incomplete.

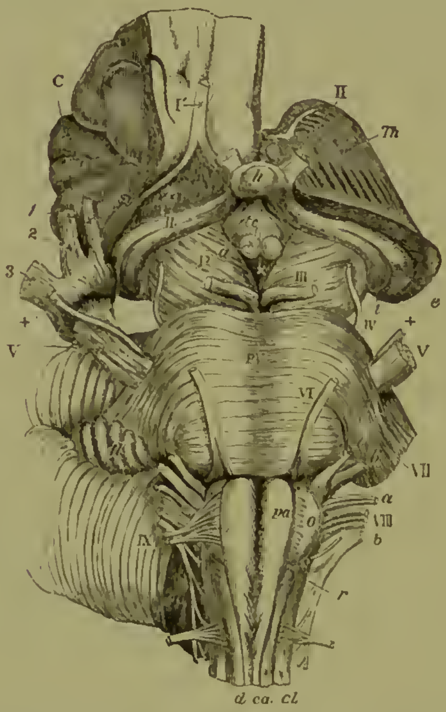


FIG. 4.—View from before of the Med. Obl., Pons Varolii, Crura Cerebri, &c. (after Quain).—On the right side the convolutions of the central lobe, or Island of Reil, have been left; on the left the incision has been carried between the optic thalamus and the cerebral hemisphere. I'. The olfactory tract cut short. II. The left optic nerve in front of the commissure. II'. The right optic tract. *Th*. The cut surface of the left optic thalamus. *c*. The Island of Reil. *Sy*. The fissure of Sylvius. XX. Locus perforatus anticus. *e*. The external, and *i* the internal corpus geniculatum. *h*. The hypophysis cerebri, or pituitary body. *tc*. Tuber cinereum and infundibulum. *a*. One of the corpora albicantia. P. The peduncle, or crus cerebri. III. Close to the left oculo-motor nerve. *x*. The locus perforatus posticus. *PV*. Pons Varolii. V. The greater root of the fifth nerve. +. The lesser or motor root; on the right side this is placed on the Gasserian ganglion. 1, 2, 3. The divisions of the fifth nerve. VI. The sixth nerve. VII *a*. The facial. VII *b*. The auditory. VIII. The pneumogastric. VIII *a*. The glosso-pharyngeal. VIII *b*. The spinal accessory. IX. The hypoglossal. *fl*. The flocculus. *pa*. The anterior pyramid. *o*. The olivary body. *r*. The restiform body. *d*. The anterior median fissure of the spinal cord, above which is the decussation of the pyramids. *ca*. The anterior column. *cl*. The lateral column of the spinal cord.

Hemisection of the medulla above the decussation of the pyramids would cause paralysis of sensation and motion on the opposite side of the body.

Emerging from the medulla oblongata the tracts pass into the *pons Varolii* (*PV*, fig. 4). Here they form connections with the grey matter of the pons, and with the transverse bundles of fibres which proceed from the lateral lobes of the cerebellum. The course of the tracts is traversed by the roots of some of the cranial nerves in their passage to the medulla oblongata. The decussation of the various sensory and motor tracts is complete in the pons, hence destruction of one side causes paralysis of motion and sensation on the opposite side, and also paralysis of the cranial nerves on the same side, which take their superficial origin here—*hémiplégie alterne* (Gubler).

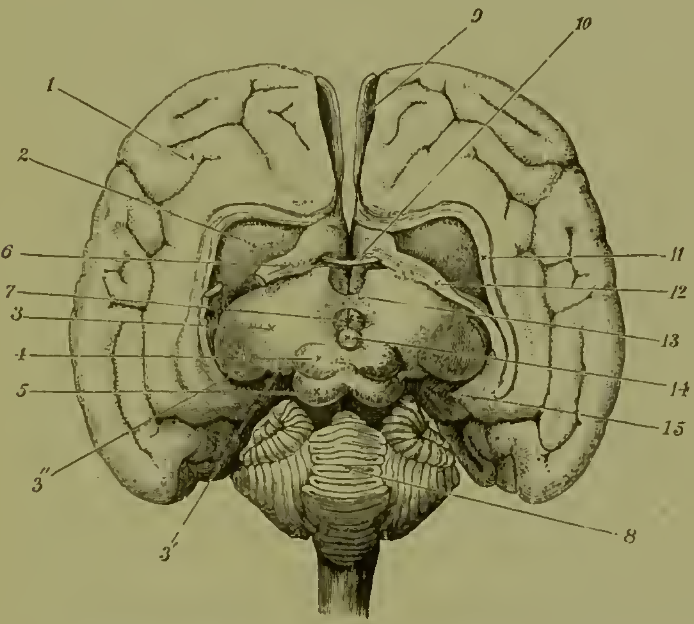


FIG. 5.—The Cerebral Hemispheres of the Dog separated after Division of the Corpus Callosum, so as to expose the Ventricles and Basal Ganglia. 1. The internal surface of the left hemisphere. 2. The corpus striatum. 3. The optic thalamus. 4. The nates, or anterior tubercles of the corpora quadrigemina. 5. The testes or posterior tubercles. 6. The anterior pillar of the fornix, which is divided on the left, undivided on the right side (12). 7. The third ventricle, exposed by drawing the optic thalami asunder. 8. The upper surface of the cerebellum. 9. The olfactory bulb or rhinencephalon. 10. The anterior commissure. 11. The corpus callosum divided. 13. The soft commissure. 14. The pineal gland, situated over and concealing the posterior commissure. 15. The descending cornu of the lateral ventricle.

Beyond the pons Varolii, and reinforced by fibres derived from it and its connections, the tracts appear as two peduncles or limbs, called the *crura cerebri* (P, fig. 4). These slightly diverge from each other in their upward course, and are traversed by the third, or oculo-motor nerves (III, fig. 4). On the posterior aspect of the crura, and anterior to the cerebellum, are situated certain ganglionic masses, termed the *corpora* *quadrigemina* or optic lobes (8, fig. 3). In the crura there is a distinct separation between the sensory and motor tracts; the lower or inferior (*crusta* or *basis*) being the motor (*g*, fig. 6), and the upper or posterior (*tegmentum*) (*r*, fig. 6) forming the sensory tracts, the two being separated from each other by a layer of dark-coloured nerve cells, called the *locus niger*. The *tegmentum* or sensory tracts also contain or enclose a mass of nerve cells called the *red nucleus*, which is in connection with the cerebellum and corpora quadrigemina.

Destruction of one crus cerebri causes paralysis of motion and sensation on the opposite side of the body, and paralysis of the third or oculo-motor nerve on the same side.

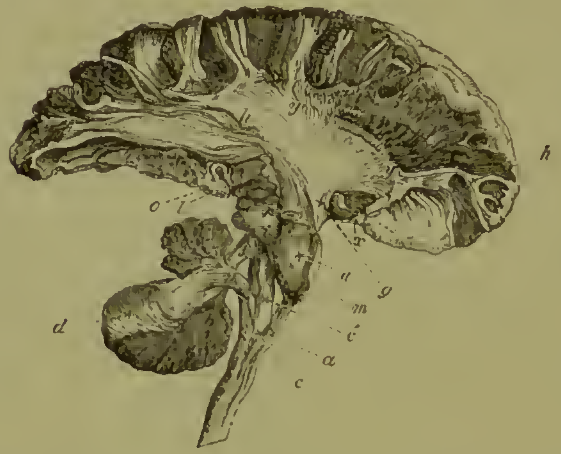


FIG. 6.—Dissection showing the connection of the columns of the Spinal Cord and Medulla Oblongata with the Cerebrum and Cerebellum (Mayo). *a*. The anterior pyramid. *a'*. Its continuation into the pons Varolii (*m*). c. The olivary body. *c'*. olivary fasciculus. *d*. White laminæ of cerebellum. *f*. Superior peduncle of cerebellum. *g*. Anterior part or *crusta* (basis) of the crus cerebri. *h*, *y*, *y*. part of the corona radiata. *i*. Fillet. *l*. Back of optic thalamus. *m* Pons. *n*. Inferior peduncle of the cerebellum. *o*. Section of the pes hippocampi. *r*. Tegmentum.

The crura cerebri pass into two great ganglia, situated at the base of the brain, and concealed or enclosed by the cerebral hemispheres. Of these *basal ganglia*, the posterior pair are called the *optic thalami* (3, fig. 5), the anterior, the *corpora striata* (2, fig. 5). The sensory tracts pass specially into the optic thalami, while the motor tracts of the crura cerebri, pass into the corpora striata. Anatomically, therefore, the optic thalami are ganglia of the tegmentum or sensory tract, and the corpora striata ganglia of the foot or motor tract.

§ 5. From these 'ganglia of interruption,' white fibres radiate into the hemispheres in the form of a hollow cone, or *corona radiata* (fig. 6, *h y y*). By means of this peduncular expansion the grey matter on the surface of the hemisphere is brought into connection with the periphery through the sensory and motor tracts, which have been traced upwards from the spinal cord.

The exact method of distribution of the fibres of the corona radiata in the several regions of the cortex has been variously given by Meynert, Broadbent, Luys, etc., but on this subject physiological experiment is more to be relied on than anatomical attempts to trace the course of individual bundles.

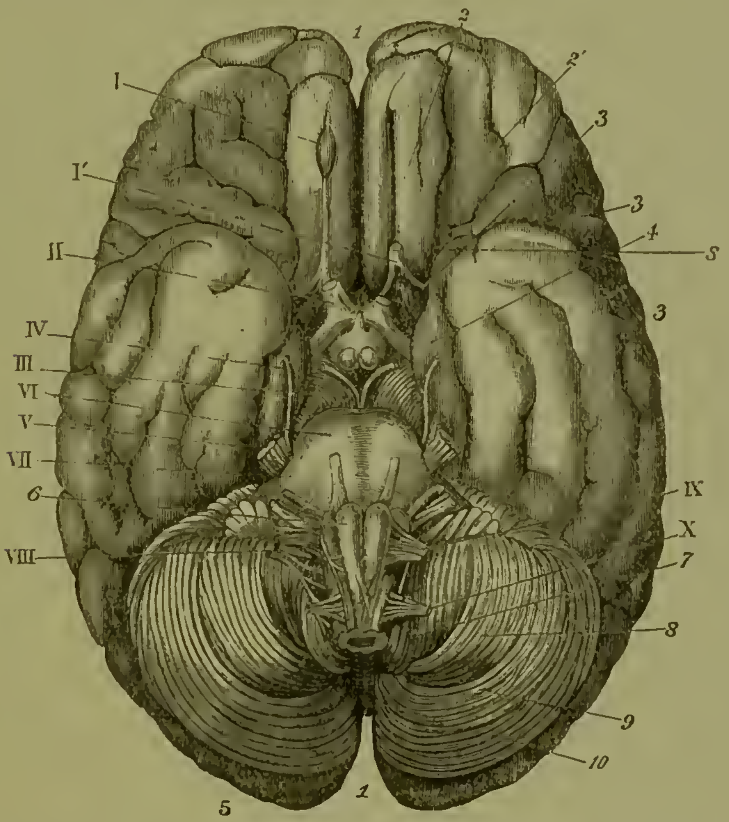


FIG. 7.—Base of the Brain. 1. Superior longitudinal fissure. 2. The fissure of the left olfactory tract, which is cut. 2′. The orbital lobe. 3, 3, 3. The fissure of Sylvius. 4. The gyrus hippocampi. *s.* The subiculum cornu Ammonis. 5. The occipital lobe. 6. The anterior pyramid of the medulla oblongata. 7. The amygdaloid lobule of cerebellum. 8. The biventral lobe. 9. The slender lobe. 10. The posterior inferior lobe. The Roman numerals I. to IX. indicate the respective cranial nerves; X is the first spinal nerve.

The cerebral hemispheres form each a sort of hollow shell, enclosing and overlapping the great basal ganglia, the inner walls being formed in great measure by the hollow cone of medullary fibres radiating in all directions from these structures.

The two hemispheres are connected together by a great body of transverse commissural fibres, the *corpus callosum* (11, fig. 5), which is brought into view by drawing asunder the two hemispheres in the middle line. This system of commissural fibres connects together corresponding regions of both hemispheres.

The corpus callosum requires to be cut through in order to display the interior of the hemispheres and the basal ganglia (fig. 5).

The form of the hemisphere is irregularly triangular, and the outer surface, which is convex, describes from the anterior or frontal extremity a curvilinear sweep backwards, downwards, and forwards, with a tending towards the mesial line, where the hemisphere ends in a rounded protuberance, which forms the extremity of what is termed the temporo-sphenoidal lobe (fig. 7, s).

The surface of the hemisphere is composed of layers of nerve cells and fibres, variously arranged in different parts of the cortex.

The accompanying figure (fig. 8) gives the microscopical appearance of a section taken from the frontal lobe.

In the brains of the rodents and the lower vertebrates (figs. 11, 12, 13, 14) the grey matter forms a smooth layer, but in the higher animals the surface is disposed in folds or convolutions separated by certain primary and secondary fissures or sulci, which have a definite position and relation to each other, as will be described subsequently. The cavity of the hemisphere follows the same general course as the curve of the hemisphere itself, and at its inner edge (fig. 5, 15), as it winds round the crus

FIG. 8.—Section of the Grey Matter of the Hemisphere taken from the third Frontal Convolution (after Meynert) × 100 diam.—1. Layer of scattered small cortical corpuscles. 2. Layer of close-set small pyramidal cortical corpuscles. 3. Layer of large pyramidal cortical corpuscles (Ammon's horn formation). 4. Layer of small, close-set, irregularly-shaped cortical corpuscles (granule-like formation). 5. Layer of fusiform cortical corpuscles (claustrum formation). *m.* Medullary lamina.

cerebri, the grey matter of the hemisphere becomes folded into the interior in a reverse manner to the surface convolutions, giving rise to an internal convolution or prominence in the ventricular cavity. This formation, which has certain peculiarities of structure, is termed the *hippocampus major*. In the brain of man and the monkey a similar internal projection is found in the cavity of the occipital lobe, and is termed the *hippocampus minor*.

The various parts of the brain are connected together by systems of commissural fibres, longitudinal and transverse.

The corpus callosum, as we have seen, is a great transverse commissure connecting corresponding regions of the cortex of both hemispheres. Underneath the corpus callosum another system of fibres is seen to ascend from the hippocampi and to converge and descend just in front of the optic thalami, into which they radiate after forming a twist or loop in the *corpora albicantia* (A, fig. 4). This system of fibres connecting the optic thalami and hippocampi is termed the *fornix* with its pillars (fig. 5, 6 and 12). Crossing the anterior pillars of the fornix, and passing through the corpora striata, a transverse band of fibres, called the *anterior commissure* (fig. 5, 10), joins the lower temporo-sphenoidal regions with each other; while some of the fibres, forming a loop, directly connect the olfactory bulbs and tracts (fig. 5, 9) with each other—an arrangement, however, which can only be distinctly traced in the lower animals with highly developed olfactory bulbs.

The optic thalami are also joined by two commissures—the *soft commissure* (fig. 5, 13) and the *posterior commissure*—on which is situated the pineal gland (fig. 5, 14).

Besides these, the various regions of the cortex are linked together by systems of 'associating fibres,' which furnish an anatomical substratum for the associated action of different regions with each other.

§ 6. The cerebellum, which occupies a position above the medulla oblongata and pons Varolii, and posterior to the corpora quadrigemina, is connected with each of these structures by what are termed its peduncles.

The form of the cerebellum varies in different animals (see

Figs. 16–25), and it is more or less divided into lobes, a median and two lateral, though the lateral lobes are not found equally developed in all classes. The surface of the cerebellum is disposed in the form of laminated folds, and the grey matter which forms the surface exhibits, on section, the appearance of leaflets (*arbor vitæ*). (See fig. 3.)

Microscopically, the grey matter is composed of a beautiful arrangement of granules, cells and nerve fibres (fig. 9).

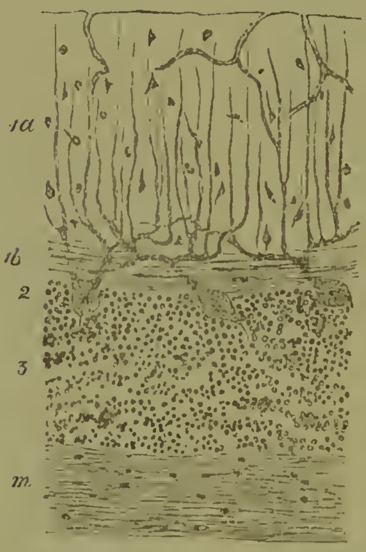


Fig. 9.—Section of the Cortex of the Cerebellum (after Meynert).—1*a*. External portion of the pure grey layer. 1*b*. Internal portion of the pure grey layer, with fusiform cells and fibræ arcuatæ. 2. The layers of Purkinje's cells. 3. The granule layers. *m*. Medullary lamina.

The interior or medulla of the cerebellum consists of fibres radiating from the peduncles, along with commissural fibres between one part of the cerebellum and another, and also of two collections of nerve cells called the *corpora dentata*, which have a special relation to the anterior peduncles.

The cerebellum is connected with the medulla oblongata by two peduncles, termed the *inferior peduncles* of the cerebellum, or *restiform tracts* (3, fig. 3; *n*, fig. 6). These are specially connected with the posterior columns of the spinal cord, through the medium of two oval-shaped ganglia termed the *olivary bodies* (*o*, fig. 4), which are developed in the medulla oblongata. From the researches of Meynert, it would appear that the connection is mainly crossed, and that, therefore, the right restiform body is connected with the opposite or left posterior column, and *vice versâ*. Whether the cerebellum is connected with the motor tracts of the spinal cord through the inferior peduncles is less certain, though fibres are described by some as connecting them with the anterior and lateral columns of the spinal cord.

The *middle peduncles* of the cerebellum (fig. 4), form the great mass of the pons Varolii. These peduncles are developed proportionately to the lateral lobes of the cerebellum. They undergo decussation in the middle line, and enter into connection with the strands which pass to the opposite cerebral hemisphere. Hence the right half of the cerebellum becomes functionally related to the left cerebral hemisphere, and a cross relation is established between the cerebral and cerebellar hemispheres.

The crura cerebri, which we have already followed, contain the longitudinal strands from the spinal cord, as well as strands derived from the cerebellar peduncles and grey centres of the pons. The cerebellum is further connected with the higher centres by means of two peduncles which emerge from its anterior aspect. These *superior peduncles*, or *processus a cerebello ad cerebrum* (5, fig. 3), enter the posterior extremity of the corpora quadrigemina, converge beneath them, and decussate into the red nuclei of the tegmenta or sensory regions of the crura cerebri. Their further destination is doubtful, though, according to Meynert, they form part of the motor division of the corona radiata. The cerebellum is directly connected with the corpora quadrigemina by a thin lamina which stretches, between the superior peduncles, from the anterior extremity of the middle lobe of the cerebellum to the posterior tubercles of the corpora quadrigemina. This lamina is called the *valve of Vieussens* in human anatomy, but in the lower vertebrates, such as the fishes, this structure is more largely developed, and is the direct connection between the cerebellum and optic lobes.

§ 7. The *corpora quadrigemina*, so called because, in the brain of mammals, they form four tubercles—*nates* and *testes*—(4 and 5, fig. 5), correspond to the *bigeminal bodies*, or *optic lobes* (figs. 11–13, A), of the lower vertebrates, a name derived from the fact that the optic tracts arise superficially from their surface.

These ganglia are connected both with the sensory and motor tracts and centres. They are in relation with the motor columns of the spinal cord on each side by a strand of fibres thrust aside by the decussation of the pyramids, and which, passing upwards and embracing the olivary body, ascends with the other longitudinal tracts through the pons, and ultimately enters the corpora quadrigemina at their inferior and lateral aspect. These two strands enter the grey matter of the corpora quadrigemina, and then decussate with each other on the upper surface, and thus form the roof of the canal, or *aqueduct of Sylvius*, which passes below these ganglia and connects the cerebral ventricles with the fourth ventricle and spinal canal (see fig. 3). The corpora quadrigemina are also structurally connected with the tegmentum and optic thalami.

From the surface of the optic lobes in the lower vertebrates, or from the surface of the anterior tubercles in mammals more especially, spring the optic tracts. These wind round the crura cerebri (II′, fig. 4) to the middle line at the base of the brain, and there undergo decussation with each other, in the *optic chiasma* or commissure. The decussation is complete in the lower vertebrates, but it is generally held to be incomplete in man. On this subject see below, p. 72.

The olfactory or first cranial nerve springs from the *olfactory bulb* (I, fig. 7), which appears at the frontal extremity of the orbital region of the hemisphere, and is connected with the hemisphere by a peduncle or tract called the *olfactory tract* (I′, figs. 4 and 7). The tract and bulb are in reality an offshoot from the hemisphere—a structural formation seen temporarily in the embryonic brain, and permanently in the brain of some of the lower vertebrates, such as the frog and turtle. In these the *rhinencephalon* (Owen) appears as a direct continuation of the hemisphere anteriorly, and contains a cavity which communicates with that of the hemisphere. In the higher vertebrates the cavity is more or less obliterated, and the rhinencephalon becomes modified into the olfactory bulb and its tract or peduncle. The connections of this with the hemisphere constitute the roots of the olfactory tract. One of these—the outer—can be followed across the *locus perforatus anticus* (XX., fig. 4) to that part of the brain which forms the lower extremity of the temporo-sphenoidal lobe. This is seen most clearly in the brain of those animals which have highly-developed tracts and bulbs, such as the rabbit (fig. 14), dog (fig. 32, o), etc., but the arrangement is the same in the simian and human brain.

The other root joins the hemisphere at its internal margin, just anterior to the optic commissure. The further course of this root is not satisfactorily traced, though Meynert would make it join the corpus striatum. By means of the anterior commissure the olfactory bulbs are joined together; and this commissure furthermore, as has been seen, connects together the parts of the hemispheres to which the outer roots are traceable. The second pair, or optic nerves, have already been partly described. In their passage round the posterior aspect of the optic thalami the optic tracts form connections with two ganglionic eminences situated at the posterior extremity of the optic thalami, and termed the *corpora geniculata* (externum and internum) (*e*, *i*, fig. 4).

The third pair of cranial nerves, or oculo-motor, and the fourth pair, or trochlear, both arise from nuclei in the corpora quadrigemina. The other cranial nerves (see fig. 4), viz. the fifth, the sixth or abducens oculi, the seventh or facial, the auditory, the vagus, the glosso-pharyngeal, the spinal accessory and the hypoglossal are all traceable to nuclei in the medulla oblongata, where anatomical connections exist between those which have associated physiological action, and where connections are formed with the strands ascending either to the cerebrum or cerebellum.

CHAPTER II.

REFLEX FUNCTIONS OF THE SPINAL CORD.

§ 8. The spinal cord, besides being the medium of communication between the brain and the periphery, possesses functions as an independent nerve centre, which have an important bearing on all investigations into the functions of the brain proper. The functions of the cord as an independent centre are of the same kind as those which we observe in their greatest simplicity in the nervous mechanism of many of the invertebrata. In the ascidians, the ancestral type of the vertebrates, the nervous apparatus consists of a central ganglion (fig. 10, *c*), connected with the periphery by two sets of nerve filaments. One set is distributed to a part of the integumentary surface capable of receiving and being acted on by external stimuli (*a*), the other is distributed to muscular fibres, which on contraction cause diminution of the body cavity (*d*). Impressions made on the sensory surface are conveyed by the afferent fibres to the central ganglion, whence an impulse is sent along the efferent fibres, causing contraction of the muscles. Such an action is termed a *reflex action*, a term derived from the reflection, as it were, of the afferent impression back to the periphery.

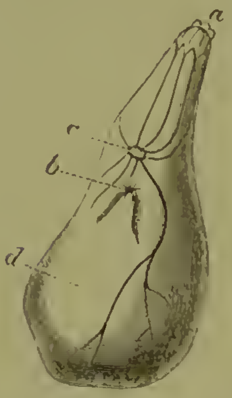


Fig. 10.—Nervous System of an Ascidian (Carpenter). *a*. The mouth. *b*. The vent. *c*. The ganglion. *d*. The muscular sac.

The spinal cord of the vertebrate animals may be looked upon in one respect as only a more complex example of an essentially similar mechanism, and may be regarded as composed of thirty-one connected segments, each of which with its pair of nerves is a bilateral repetition of the central ganglion, with its afferent and efferent fibres. If the body of a frog be divided transversely, the lower half will still retain its vitality for a considerable period, and continue to manifest the same kind of action which is observed in the case of the ascidians. If the foot be irritated, the muscles of the leg will be thrown into action, and this will occur so long as the grey matter of the cord is intact, and its connections with the periphery are maintained. The impression on the sensory surface is conveyed to the cord, and there originates an impulse, which travelling outwards along the efferent nerve, excites the muscles to contraction. This is an example of the reflex function of the spinal cord, which Marshall Hall was the first distinctly to formulate. After section of the cord in warm-blooded animals, the same reflex contraction of the muscles is caused when a part is irritated below the line of section. A similar experiment is frequently performed by disease in man. When, as the result of injury or disease, there is a solution of the continuity of the cord at any point, all the parts deriving their nervous supply from the cord below the seat of lesion become paralysed, both as regards voluntary motion and sensation. If, however, the soles of the feet be tickled, the legs will be thrown into convulsive action, of which the individual is not conscious, and which it is out of his power in the slightest degree to control. Here we have to deal with phenomena of a purely reflex character, and the experiment has an important bearing on our interpretation of these and similar phenomena in the lower animals, as showing that consciousness is not necessarily a concomitant of reflex action. If the brain and cord are connected, and if the brain is in a state of wakeful activity, the same stimulus which gives rise to reflex muscular action will also excite sensation, but this is no essential factor in the process. If the soles of the feet of a person asleep be tickled the legs will be withdrawn, or if a finger be placed in the palm of a sleeping child the fist will close on it, but in neither case is there any consciousness of the tactile impression.

Though the spinal cord acts as a centre of reflex action, either in union with, or after severance from, the brain, the brain exerts a powerful influence over the phenomena. Thus, by a strong effort of the will, some persons may succeed in restraining the movements of the legs which would otherwise result from tickling the soles of the feet. And it has been proved experimentally in the lower animals, that the encephalic centres exercise a restraining or inhibitory influence over the reflex action of the cord. This has been ascertained in the following manner. A frog is suspended by the head, and the legs, which hang down, are allowed to dip into a vessel containing dilute acid. After a certain interval the irritation of the acid causes the legs to be withdrawn. The average interval is determined by repeated trials. The same experiment is again performed after division of the cord below the medulla oblongata. The interval which now elapses between the contact with the acid and the withdrawal of the feet is considerably shortened, and the action is observed to be more energetic.

Setschenow ('Phys. Stud. über die Hemmungsmechanismen,' 1863) has further shown that this inhibitory influence of the encephalic centres on the reflex functions of the spinal cord, can be intensified by direct irritation of the optic lobes. By suspending a frog in the above-mentioned manner, and at the same time applying chemical irritation to the surface of the optic lobes, he found that the interval between the contact with the acid and the reflex muscular contraction was greatly prolonged. This inhibitory influence of higher over lower nerve centres we shall see reason to extend into the region of the encephalic centres themselves.

(The nature of the inhibitory mechanism is exceedingly obscure. For an elaborate disquisition on this subject, see a paper by Dr. Lauder Brunton, in the 'West Riding Reports,' vol. iv.: 'Inhibition, Peripheral and Central.')

§ 9. The conditions and character of the phenomena of reflex action deserve more particular consideration. The extent and nature of the movements vary with the degree and mode of stimulation. As a rule, a moderate stimulus excites reflex action on the same side as that to which the stimulus is applied. Thus, a gentle irritation of one foot will cause withdrawal of that leg alone. If, however, the stimulation is more intense, there is an irradiation in the grey matter of the cord, and the muscular contractions are no longer confined to one group or one limb, but occur on both sides, and in all four limbs. A similar result follows, if in place of the irritant being intensified, the reflex excitability of the cord is heightened. Thus, in certain forms of disease, and as the result of strychnine poisoning, the reflex excitability of the cord is increased, and the resistance to radiation diminished, so that an amount of irritation which, in the normal condition, would only excite limited muscular action, is sufficient to induce reflex spasms of a general character.

Though as a rule the summation of stimuli increases the reflex action and makes it more general, this is only true of stimuli conveyed to the same part of the cord (Wundt). If, on the other hand, a sensory nerve in some other part of the body is simultaneously irritated, then the reflex action which would otherwise result from the first stimulus is altogether restrained or inhibited (Herzen, Schiff).

This phenomenon seems to be of a similar nature to that which results from irritation of the optic lobes, or optic thalami in Setschenow's experiments; and it would appear that reflex action in general is inhibited when simultaneous impressions of different origins are made on the nerve centres.

Thus far we have confined our attention merely to the general fact of reflex action, and some of the conditions of its manifestation. We have to consider more specially the characters of the phenomena so excited reflexly.

They are not mere muscular contractions of an aimless character, but possess all the distinctive features of adapted movements, and this to such an extent as to have given rise to considerable discussion as to whether intelligence may not really be concerned in their causation. They are movements either of defence or preservation, and are in general adapted either to withdraw the part from the source of irritation, or to repel the irritant itself. Thus, the extended leg becomes flexed, or withdrawn, when the toe is pinched, and if the irritant be applied to the anal region, adapted movements of both legs are made, with a view to remove it.

But special adaptations to special circumstances of a very remarkable kind, may likewise be manifested by the spinal cord, as are illustrated by Pflüger's well-known experiments ('Die Sensorischen Funktionen des Rückenmarks,' 1853).

When a drop of acetic acid is placed on the thigh of a decapitated frog, the foot of the same side is raised, and attempts made with it to rub the part. On the foot being amputated, and the acid applied as before, the animal makes a similar attempt, but failing to reach the point of irritation with the stump, after a few moments of apparent indecision and agitation, raises the other foot, and attempts with it to remove the irritant.

This experiment has been appealed to by Pflüger and others as a proof of psychical or intelligent action on the part of the spinal cord. There is no more difficult problem in the physiology of the nerve centres, than to distinguish between the phenomena of purely reflex action and those of consciousness, sensation, and intelligence ; a difficulty which becomes greater when we ascend to the encephalic basal ganglia. The existence of consciousness in others is only an inference from our own experience, and we are inclined to attribute to consciousness, such actions as necessarily imply distinct sensation and intelligent action on our own part. It is, however, an established fact, that adapted actions, such as intelligence would also dictate, are capable of being called into play through our spinal cord, entirely without consciousness. This alone, apart from other considerations, would lead us to look upon the more complex adapted actions performed by the spinal cord of animals lower in the scale, but whose cerebro-spinal system is of exactly the same type as our own, as differing in *degree* only, and not in *kind*, from the phenomena of reflex action in our own spinal centres. The facts described by Pflüger do not seem to require any other interpretation. Though the irritation caused by a drop of acid usually at first only causes movements of the same limb, I have not unfrequently observed both legs simultaneously brought up to the same part, with a view to repel the cause of offence. In this we have an instance, among many others, in proof of the physiological association in the spinal cord between the centres of movements of the same kind in both limbs, due either to their commissural connections, or the organisation of past experience (Lotze), or both together. Such being the case, it is not difficult to conceive that when the relief afforded by scratching at or near the part is not attained, owing to the amputation of the foot in Pflüger's experiment, the continuance of the irritation brings the other leg into play by associated reflex action. It is not even necessary to amputate the foot, for after repeated stimulation of the same point, the leg of the same side becomes exhausted, whereupon the other foot is brought up to the part on each re-application of the stimulus. Goltz ('Beiträge,' &c., 1869) has shown by a series of ingeniously contrived experiments, that the apparently purposive movements of the decapitated frog, excited by peripherical stimulation, vary in character with the seat and nature of the irritation, but that none of them transcend the ordinary character of adapted reflex actions. He has, further, furnished a strong argument against attributing a sensory function to the spinal cord, by the following among other experiments.

He took two frogs, one of which was decapitated, the other intact, except that it was blinded in order to prevent the occurrence of voluntary movements consequent on visual sensation.

Both were placed in a vessel of water, and the temperature gradually raised. Both remained still until the temperature reached 25° C. The frog with brain uninjured, began to manifest signs of discomfort, which were succeeded by attempts to escape as the temperature rose, until finally it died of tetanic heat rigidity at a temperature of 42° C. All this while the brainless frog sat perfectly still, showing no signs of uneasiness or pain. But—and it is worthy of note—while sitting in the hot water it made the usual reflex defensive movements when acetic acid was applied to the skin. Beyond this it remained quiet, and died of heat rigidity at 50° C. Here we have a proof, apparently as conclusive as can well be, that a frog without its brain, and capable of reflex action, is perfectly insensible to what in the normal state gives rise to signs of pain. Though the outward signs of pain need not indicate consciousness of pain, yet the absence of any such signs is a proof that no painful sensation is experienced.

§ 10. The phenomena of reflex action of an adaptive character dependent on the spinal cord, are exemplified also in the functions of organic life. Reflex contraction of the visceral muscles is caused by stimulation of their corresponding afferent nerves, such as may be seen in the mechanism of the retention and expulsion of secretions. Between the nervous mechanism of the visceral and animal functions intimate relations exist. Reflex movements of the viscera may be produced by stimulation applied to certain cutaneous surfaces, and conversely, irritations of visceral surfaces are capable of being transferred to the muscles of animal life, a connection which serves to explain many phenomena of disease—*sympathies* (*synæsthesiæ*, *synkinesiæ*).

§ 11. What is termed the *automatic action* of the spinal cord is in a great measure reflex action of a constantly operative character. This so-called automatic action is exemplified in the maintenance of the *tone* of the sphincters, partly in the tone of the blood-vessels (Vulpian), and in the tone of the muscles generally. The tonic contraction of the sphincters keeps the orifices closed until they are forced by stronger muscular efforts, voluntary or involuntary. The tone of the muscles is a constant contraction or tension, which is manifested more particularly when their antagonists are paralysed. If the extensor muscles of a limb are paralysed, by section of their nerves for instance, the tonic contraction of the flexors causes permanent flexure of the limb. In like manner, when one set of bilaterally acting muscles becomes paralysed, the tonic contraction of the others causes lateral distortion.

That this tone is in a great measure due to latent centipetal influences constantly proceeding from the periphery, is shown in the case of the sphincters, by the fact that they close more firmly when the mucous orifices they guard are stimulated, as by an attempt to force them; and also by the fact, first pointed out by Brondgeest (Reichert's u. Du Bois Reymond's 'Archiv,' 1860), that when the afferent nerves are cut, the tone disappears. The same principle of latent reflex stimulation is applicable to the tone of the animal muscles. This fact of latent reflex action seen in the spinal cord, has a very important bearing on the signification of certain phenomena of experimentation on the higher encephalic centres.

In some cases, however, there would seem to be manifestations of functional activity, conditioned by the state of nutrition and circulation in the spinal centres, independently of peripherical stimuli, and to these alone the term automatic would be strictly applicable.

The functions of the spinal cord in reference to nutrition and secretion, do not fall within the scope of the present inquiry.

(See an able historical and critical analysis of the 'Reflex Functions of the Spinal Cord,' by Dr. W. Stirling, 'Edin. Med. Jour.,' April and June 1876.)

CHAPTER III.

FUNCTIONS OF THE MEDULLA OBLONGATA.

§ 12. When we pass from the spinal cord to the medulla oblongata, we come to a centre of reflex co-ordination of a more complex character, and more intimately related to essential vital functions.

With the exception of the first four, all the other cranial nerves are directly connected with the grey centres of the medulla oblongata, and from this anatomical disposition alone, we might infer, from the analogy of the spinal centres, that the medulla oblongata would be the centre of reflex co-ordination of such actions as are manifested in the regions of distribution of these various nerves, singly or combined. That this is the case, is abundantly proved by the facts of physiology and pathology.

Should all the encephalic centres above the medulla oblongata be removed, the mutilated organism, even of a warm-blooded animal, though deprived of the faculty of spontaneous or voluntary motion, will continue to live and breathe. Spinal reflex actions will continue to be manifested as before, and reflex actions will be called forth by stimulation of regions deriving their nervous supply from the medulla. Thus, the eyelids will close if the conjunctiva be touched; the facial muscles contract, the ear twitch and the tongue move on irritation of the sensory nerves of these various parts.

But co-ordinated actions of a much more complex nature than these are capable of being called forth. If a morsel of food be placed on the back of the tongue, the combined action of the muscles of the lips, tongue, palate and pharynx, concerned in the mechanism of deglutition, will be excited to action with as great precision as before. In a young animal so mutilated, the introduction of the nipple between the lips will excite the movements of sucking and deglutition.

A mutilation of this nature is sometimes observed in man in the case of anencephalous monsters, infants in which the centres above the medulla are undeveloped. Such infants suck and swallow as perfectly as the fully-developed child, when put to the breast. The medulla oblongata is the co-ordinating centre of these associated movements. Destruction of the medulla causes their instant annihilation. The various afferent and efferent nerves concerned in the mechanism, viz., the glosso-pharyngeal, the hypoglossal, the facial and the fifth, all spring directly from the medulla oblongata. The individual nuclei of these nerves are associated together, but anatomical investigation has not yet succeeded in explaining how their joint and harmonious action is regulated.

Though it is not possible to obtain direct experimental proof that the medulla oblongata is the co-ordinating centre of the various muscular movements concerned in the production of articulate speech, yet this is rendered probable on other grounds. The muscles concerned in articulation are directly innervated from the medulla oblongata, and the individual nuclei of these various nerves are anatomically connected with each other. In the disease known as *Duchenne's paralysis*, *glosso-labio-laryngeal* paralysis, or more shortly, *bulbar-paralysis*, there is a remarkable selection, as it were, by the diseased process of the centres of innervation of the muscles of articulation, so that there is gradual and progressive paralysis of the tongue, palate, lips and laryngeal muscles, rendering articulation, and ultimately deglutition, impossible. The disease is found to affect the centres or nuclei of the hypoglossal, facial, accessorio-vagus and glosso-pharyngeal, which undergo progressive degeneration. This selection indicates a functional as well as an anatomical correlation of these various centres, but how they are co-ordinated remains unsolved. Schroeder van der Kolk was of opinion that the connections of the hypoglossal, facial and fifth nerves with the olivary bodies (*o*, fig. 4) pointed to these ganglia as the co-ordinating centres of articulation.

More recent anatomical investigation into the minute structure of the medulla oblongata has not, however, confirmed the views of Schroeder van der Kolk, and it would appear from the researches of Meynert, already alluded to (p. 12), that the olivary bodies have more special relation to the posterior columns of the spinal cord and inferior peduncles of the cerebellum. Vulpian, moreover, relates a case of complete degeneration of the olivary bodies in which there was no affection of articulation. Though Schroeder van der Kolk's views are not confirmed either by histological researches or by pathology, we have not arrived at a positive solution of the mechanism of the co-ordinating centres of the medulla oblongata.

§ 13. The medulla oblongata is, further, a centre of the reflex manifestation of facial expression, and some other forms of what is usually regarded as emotional expression. Vulpian has shown that if a young rat be deprived of all the encephalic centres above the medulla, and if then the toes are pinched, not only may reflex movements of the limbs be produced, but also a cry, as of pain, may be elicited. This is capable of frequent repetition. If now the medulla oblongata be destroyed, pinching of the toes will cause the reflex movements of the limbs as before, but no cry will be elicited. The cry in this case is a purely reflex phenomenon, and is easily accounted for, when it is remembered that a cry is only a modified expiration, and that the medulla oblongata is the co-ordinating centre of the respiratory movements. The co-ordination of respiratory movements is one of the chief functions of the medulla oblongata. So long as the medulla is intact, the function of respiration goes on in an automatic or reflex manner, with the greatest regularity and rhythm. When the medulla is destroyed, respiration ceases and death ensues, except, as in the case of the frog, where the animal can live by cutaneous respiration.

The co-ordinating centre of the respiratory mechanism has been experimentally fixed by Flourens in the V-shaped apex of the fourth ventricle, or beak of the calamus scriptorius (4, fig. 3). This point he terms the *nœud-vital.* In this region are co-ordinated the various afferent and efferent nerves concerned in the respiratory mechanism. From this centre proceed the impulses to co-ordinated action of the thoracic walls, diaphragm and respiratory passages. If the spinal cord be severed above the origin of the phrenic nerve, the thoracic muscles and diaphragm cease to act as respiratory muscles. Simple and uncombined reflex contraction of these muscles may, however, be excited by stimulation of their corresponding afferent nerves, but they no longer act consentaneously for purposes of respiration.

In like manner, section of the medulla above the respiratory centre interrupts the efferent paths to the muscles of the respiratory orifices, but leaves unaffected the diaphragmatic and costal movements.

The afferent impressions which excite the respiratory centres to rhythmical action, are conveyed chiefly by the branches of the vagus distributed to the lungs and air passages. The condition of the lung at the close of expiration generates the stimulus to the inspiratory movements, and the distended condition of the lung at the close of inspiration excites the expiratory movement actively, or, by inhibiting the inspiratory action, allows the thorax passively to collapse.

The respiratory centre is, further, in reflex connection with the sensory nerves in general, and in particular with those of the face and chest. Hence, a sudden stimulus to these surfaces, such as a dash of cold water or a sharp flick, causes active respiratory action. But a sudden stimulation of any cutaneous surface exerts a powerful influence on the respiratory centre, causing spasmodic arrest of the respiratory movements either in the state of inspiration, or, it may be, in the state of expiration. The rhythmical alternation of expiratory and inspiratory movements is not dependent on reflex excitation alone. Respiratory movements may continue after all afferent nerves connected with the centre have been divided. In this case there is a true automatic activity conditioned by the state of the blood itself. The diminution of oxygen and accumulation of oxidation products in the blood act as a stimulus to the inspiratory centre, and this again reflexly excites the expiratory movements. When the blood is artificially hyperoxygenated, the movements of respiration come to a complete standstill, a condition termed apnœa. Nonaëration of the blood, resulting from obstruction of the function of respiration, powerfully excites the movements both of inspiration and expiration, and ultimately, if the obstruction is not overcome, causes general convulsions of the whole body, as in asphyxia. The respiratory mechanism, though essentially reflex in character, is to a great extent under the control of the will. It is by the voluntary control we exert over the respiratory movements, that we are enabled to combine them with the movements of articulation for purposes of speech and vocalisation; and in a similar manner, by closure of the glottis and forcible contraction of the expiratory muscles, we can bring the mechanism to bear, for the purpose of expelling the contents of the rectum and urinary bladder. Our voluntary control over the respiratory movements is, however, of a limited extent. If the inspiration is delayed beyond a certain point, the *besoin de respirer* becomes so urgent, that voluntary control is no longer capable of restraining the reflex or automatic activity of the respiratory centres.

Modifications of the respiratory movements are seen in the acts of sneezing and coughing. An irritation of the nasal passages excites reflexly a sudden inspiration, closure of the glottis and then a forcible expiratory explosion of the air through the nasal passages. In like manner, an irritation of the laryngeal or bronchial passages, causes a sudden explosive expiration, termed a cough. The mechanism of a cough can be imitated voluntarily, but sneezing is a purely reflex act and cannot be imitated by voluntary effort.

The path by which the respiratory centre centrifugally excites the respiratory muscles, is placed by Bell, and also by Schiff, in the lateral columns of the medulla and cervical portion of the spinal cord, and hence these are sometimes termed the *respiratory columns*. According to Schiff, section of the cervical lateral columns specially causes paralysis of the diaphragmatic and costal movements on the same side; but neither Vulpian nor Brown-Sequard have been able to substantiate any special interference with the respiratory movements after section of these columns. From their researches it would seem more probable that the connection of the respiratory centre with the centres of origin of the respiratory motor nerves, is through the grey matter of the cord itself.

The respiratory centre retains its activity long after the reflex excitability of the spinal cord is abolished, and all voluntary or conscious action has ceased. This is shown by the action of such agents as chloroform. When pushed to their full extent, they paralyse the brain and cord before the respiratory centres.

§ 14. The medulla oblongata is, further, a centre of innervation of the heart.

The rhythmical movements of the heart are independent of the medulla oblongata or cerebro-spinal centres generally, and are conditioned by the ganglia of the heart itself. Hence, the heart will continue to beat rhythmically, after complete severance of its cerebro-spinal connections, or, in cold-blooded animals, after removal from the body.

But the action of the heart is capable of being considerably modified through the nerves which connect it with the medulla.

These nerves have opposite functions, the one set *accelerating*, the other *inhibiting* or restraining, the heart's action.

The *inhibitory* branches pass from the medulla to the heart in the vagus or pneumogastric. Stimulation of the trunk of the vagus, or of the distal end of the cut trunk, or of the vagus centre in the medulla oblongata, causes the heart to stop in the state of diastole. A greater or less degree of inhibition of the heart's action is constantly maintained by the medulla; hence section of the vagi causes acceleration of the heart's action.

The *accelerator* or motor nerves of the heart pass from the medulla down the spinal cord, and reach the heart through the last cervical and first dorsal ganglia of the sympathetic nerve.

Both these sets of nerves are capable of being excited to action reflexly by stimulation of certain afferent nerves.

The inhibitory nerves may be stimulated, and the heart made to stop, by powerful irritation of the sensory nerves of the surface generally; by irritation of the sensory branches of the fifth in the nostrils (Hering); by irritation of the sensory nerves of the larynx; and in particular, by irritation of the intestinal nerves. Thus, a smart tap on the intestines of the frog causes the heart to stop (Goltz), a fact which serves to explain the danger of blows on the epigastrium, and the fatal consequences which sometimes follow the sudden shock of a large draught of cold water or irritant poison on the sensory nerves of the stomach.

The accelerator nerves can be excited reflexly by stimulation, among others, of the afferent nerves of the muscles, a fact which may partly explain the increased rapidity of the heart's action during active muscular contraction.

§ 15. The blood-vessels are also under the control of the medulla. The centre of innervation of the blood-vessels is termed the *vaso-motor* centre. The vaso-motor nerves pass by the spinal cord to the blood-vessels through the ganglia and fibres of the sympathetic system. These nerves are in a state of constant activity, and keep up a tonic contraction of the arterial walls, a condition which is termed *arterial tonus.* Hence, a section of the spinal cord below the medulla oblongata, causes cessation of the arterial tonus, and the blood-vessels become dilated.

The same result follows section of the sympathetic nerves, or section of the nerves which convey the filaments of the sympathetic to the blood-vessels. The position of the vaso-motor centre appears, from the researches of Ludwig and Owsjannikow, to be situated in the grey matter on each side of the median line of the floor of the fourth ventricle, extending from about four millimetres in advance of the beak of the calamus scriptorius to within one millimetre posterior to the corpora quadrigemina. Section above this latter point does not cause dilatation of the blood-vessels, while section posterior to the lower margin of the centre causes their complete and permanent paralysis. Vulpian, however, has shown that, in addition to the vaso-motor centre proper, the spinal cord is concerned in the maintenance of arterial tonus. This he deduces from the fact, that after section below the vaso-motor centre, a further dilatation of the blood-vessels is caused when the spinal cord is destroyed, or the anterior roots of the spinal nerves divided.

The vaso-motor centre is in relation with afferent nerves, which either excite or depress its activity, and thus reflexly cause contraction or dilatation of the blood-vessels.

Those which on irritation excite the vaso-motor centre, and thus cause contraction of the blood-vessels, are sometimes termed *pressor* nerves. These, according to the researches of Miescher, pass up the cord in the posterior part of the lateral columns.

Any sensory nerve may convey a stimulus to the vaso-motor centre. Irritation of a sensory nerve causes general contraction of the blood-vessels.

Along with this general excitation, however, there is local inhibition of the arterial tonus, so that the blood-vessels of the part immediately irritated become dilated, and the skin reddened. A similar local inhibition or dilatation of blood-vessels is observed in the stomach, on irritation of the branches of the vagus distributed to the mucous membrane of the stomach (Rutherford).

Besides these instances of local inhibition, general inhibition of the activity of the vaso-motor centre may be caused by irritation of one of the branches of the vagus which is sent to the heart.

This branch is named the *depressor* nerve, because on irritation it causes cessation of the arterial tonus and great lessening of the blood pressure. Apparently, this nerve is stimulated by laboured and distended conditions of the ventricular cavities, and thus dilatation of the blood-vessels and relief of the tension are brought about.

By the reciprocal relations which subsist between the centres of innervation of the heart and blood-vessels, variations in the blood pressure are kept within limits. A dilated condition of the blood-vessels, which would cause great lowering of the blood pressure and seriously affect the circulation, is compensated for by an increased activity of the heart. So, a contracted state of the blood-vessels, which would cause great rise in the blood pressure, is compensated for by an inhibition or slowing of the heart's action. By these means great variations from the normal standard are counteracted.

Reciprocal relations also subsist between the vaso-motor, cardiac and respiratory centres. Hence, oscillations of the pulse and blood pressure accompany the respiratory movements, quite independently of any mechanical effect of the movements of the chest on the heart; the pulse being quickened during inspiration and slowed during expiration.

The medulla oblongata is thus a co-ordinating centre of reflex actions essential to the maintenance of life. If all the centres above the medulla be removed, life may continue, the respiratory movements may go on with their accustomed rhythm, the heart may continue to beat, and the circulation be maintained; the animal may swallow if food be introduced into the mouth, may re-act to impressions made on its sensory nerves, withdrawing its limbs or making an irregular spring if pinched, or even utter a cry as if in pain, and yet will be merely a non-sentient, non-intelligent, reflex mechanism.

CHAPTER IV.

FUNCTIONS OF THE MESENCEPHALON AND CEREBELLUM.—GENERAL.

§ 16. We may now proceed to the consideration of those parts of the encephalon which lie between the cerebral hemispheres and the medulla oblongata, comprising the *pons Varolii*, *corpora quadrigemina* and *cerebellum*. It will be advantageous to consider them first in their totality, and next as regards their individual functions, in so far as these are capable of differentiation from each other.

We have already briefly discussed the actions of which an animal is capable in which all the centres above the medulla oblongata have been removed, and we have endeavoured to allot to the medulla and cord the functions proper to each. In a similar manner the functions of those parts of the encephalon now under consideration may be determined by a study and analysis of the forms of activity which are manifested by animals, from which all the centres situated in advance of the corpora quadrigemina or optic lobes have been removed.

Of experiments of this kind multitudes have been performed, with a tolerably uniform agreement as to results; though as regards their interpretation and significance, there is not the same unanimity of opinion. It is to the researches of Flourens ('Recherches Expérimentales sur les Propriétés et les Fonctions du Système Nerveux,' 2nd ed., 1842) and Longet ('Traité de Physiologie,' 2nd ed., 1866) that we owe our chief knowledge of the results of ablation of the cerebral hemispheres, though much has been added by subsequent investigators, mainly of the French school of physiology, prominent among whom stands Vulpian ('Leçons sur la Physiologie du Système Nerveux,' 1866).

The phenomena manifested by animals deprived of their cerebral hemispheres vary considerably in the different classes of vertebrate animals; differences which mainly depend on the degree of solidarity, as Vulpian well expresses it, which subsists between the individual centres of the cerebro-spinal system, according as we ascend or descend the animal scale.

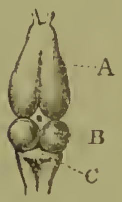


Fig. 11.—Brain of Frog. A. Cerebral hemisphere. B. Optic lobes. C. Cerebellum.

§ 17. In the case of the frog deprived of its cerebral hemispheres (A, fig. 11), the following are among the chief phenomena which are observed. (On this subject see particularly the researches of Goltz—'Functionen der Nervencentren des Frosches,' 1869). Deprived of its cerebral hemispheres, the frog will maintain its normal attitude, and resist all attempts to displace its equilibrium. If laid on its back, it will immediately turn on its face, and regain its station on its feet. If placed on a board, and the board be tilted in any direction, the animal will make the appropriate bodily movements to throw its centre of gravity within the base of support. If its foot be pinched, it will hop away. If it is thrown into the water, it will swim until it reaches the side of the vessel, and then clamber up and sit perfectly quiet. If its back be stroked gently, it will utter loud croaks, and this with such uniformity on each application of the stimulus, that, as Goltz indicates, a chorus of brainless frogs might be obtained which would utter their *βρεκεκεκέξ κοάξ κοάξ* on the appropriate occasion in a manner which would have delighted the heart of Aristophanes. Indeed, in many respects, it would be difficult to say that the removal of the hemispheres had caused any alteration in the usual behaviour of the animal. If placed in a vessel of water, the temperature of which is gradually raised, it will not quietly submit to be boiled like a frog which has only its medulla and spinal cord, but will leap out as soon as the bath becomes uncomfortably hot. If placed at the bottom of a pail of water, it will ascend to the surface to breathe. And not merely so, but if placed in a vessel inverted over a pneumatic trough, and containing a column of water sustained by barometric pressure, it will ascend to the surface as before; but not finding there the necessary atmospheric air, it will work its way downwards, and succeed in making its escape out of the vessel to the free surface of the trough. There is a method in its movements. If an obstacle be placed between it and the light of a window, the frog will not spring blindly against the obstacle when its toe is pinched, but will clear it, or spring to the side. It will alter the course of its leap according to the position of the obstacle between it and the light. There is, so far, no difference between its behaviour and that of a frog in full possession of all its faculties. But yet a very remarkable difference is perceptible. The brainless frog, unless disturbed by any form of peripherical stimulus, will sit for ever quiet in the same spot, and become converted into a mummy. All spontaneous action is annihilated. Its past experience has been blotted out, and it exhibits no fear in circumstances which otherwise would cause it to retire or flee from danger. It will sit quite still if the hand be put forth cautiously to seize it, but will retreat if a brusque movement is made close to its eyes. Surrounded by plenty it will die of starvation; but unlike Tantalus, it has no psychical suffering, no desire, and no will to supply its physical wants.

§ 18. The results which have been observed in fishes after similar ablation of the cerebral hemispheres (A, fig. 12), are, *cæteris paribus*, of the same nature as those seen in frogs. A fish so mutilated maintains its normal equilibrium in the water, and uses its tail and fins in swimming with as great precision and co-ordination as before. The brainless fish is, however, continually on the move, and there is also method in its movements. It will not run its head against any obstacle placed in its path, but turn to the right or left according to circumstances. Left to itself in the water, it swims in a straight line, and, unlike other fishes which loiter by the way, smelling at this and nibbling at that, it keeps on its course, as if impelled by some irresistible impulse, and only stops when it reaches the side of the vessel, or when worn out by pure nervous and muscular fatigue. Apparently there is some essential difference between the frog, which sits for ever quiet, and the fish which goes on indefinitely, but the same explanation is applicable to both (p. 41).

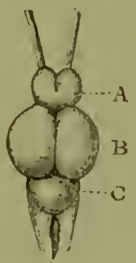


FIG. 12.—Brain of Carp. A. Cerebral hemisphere. B. Optic lobes. C. Cerebellum.

Like the frog, the fish perishes of starvation, surrounded by abundant supplies of otherwise tempting food.

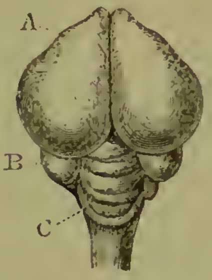


FIG. 13.—Brain of the Pigeon. A. Cerebral hemisphere. B. Optic lobes. C. Cerebellum.

§ 19. The results of removal of the cerebral hemispheres in pigeons have been described in great detail by Flourens, Longet, Vulpian, &c. A pigeon so mutilated continues able to maintain its equilibrium, and to regain it when disturbed. When placed on its back it succeeds in regaining its feet. When pushed or pinched it marches forward. Should it happen to step over the edge of the table it will flap its wings until it regains a firm basis of support. When thrown in the air it flies with all due precision and co-ordination. Left to itself it seems as if plunged in profound sleep. From this state of repose it is easily awakened by a gentle push or pinch, and looks up and opens its eyes. Occasionally, apparently without any external stimulation, it may look up, yawn, shake itself, dress its feathers with its beak, move a few steps, and then settle down quietly, standing sometimes on one foot and sometimes on both. Should a fly happen to settle on its head it will shake it off. If ammonia be held near its nostrils it will start back. Should the finger be brusquely approximated to its eyes it will wink and retreat. A light flashed before its eyes will cause the pupils to contract; and if a circular motion be made with the flame the animal may turn its head and eyes accordingly. It will start suddenly and open its eyes widely if a pistol be discharged close to its head.

After each active manifestation called forth by any of these methods of stimulation, the animal again subsides into its state of repose. It makes no spontaneous movements. Memory and will seem annihilated. When irritated it may show fight both with wings and beak, but it exhibits no fear and makes no attempts at escape. It resists attempts to open its beak for the purpose of introducing nourishment, but should its resistance be overcome, it swallows as usual. If fed artificially it may be kept alive for months, but left to itself it will die of starvation, like the frog or fish.

Such are the chief phenomena observable in the case of these animals, according to the researches of Flourens, Longet, Vulpian, Goltz, Rosenthal, and myself; but it is worthy of remark that Voit, on the strength of some experiments of his own on pigeons, has controverted the usually accepted view that these animals, deprived of their cerebral hemispheres, cease to manifest spontaneous or voluntary action. He says he has seen them walk about and fly of their own accord, and only differ from other pigeons in not being able to feed themselves. There is good reason, from Voit's own account of the regeneration of the hemispheres in one of his pigeons, for attributing the phenomena of spontaneous action which he describes to incomplete removal of the hemispheres. In this way only can we account for statements so directly opposed by the observations of so many others who have performed similar experiments.

§ 20. When we pass from the consideration of the functions which the lower centres in frogs, fishes and birds are capable of performing, independently of the cerebral hemispheres, to the effects of removal of the hemispheres in mammals, we have to deal with phenomena of a more varied character. We have seen that frogs, fishes and birds, deprived of their cerebral hemispheres, continue to perform actions in many respects differing little, if at all, from those manifested by the same animals under absolutely normal conditions. But the results, in the case of mammals, are far from exhibiting the same degree of uniformity. Differences of a marked character exist, according to the age of the animals experimented on, and the order to which they belong. If we were to draw conclusions from experiments on one order of animals, and extend them, without due qualification, to animals in general, and particularly to man, we should be in danger of falling into serious errors. The neglect of such considerations has been a fruitful source of discrepancies and contradictions between individual physiologists, and between the facts of experimental physiology and those furnished by clinical and pathological research.

Though we may take it as an important guide in our inquiries, that nerve centres constructed on the same type perform homologous functions, yet, as we ascend the animal scale, the centres of which the cerebro-spinal system is composed become more and more intimately bound up and associated with each other in action, so that to separate the one from the other involves such functional perturbation of the whole, that only in rare instances is it possible to obtain indications of independent activity on the part of those which are not directly injured. That such is the case will be abundantly illustrated as we proceed.

Among mammals, rabbits and guinea-pigs have been the favourite subjects of physiological research; and of these, those of tender age are best adapted for the purpose, on account of the lesser degree of solidarity which subsists between their several encephalic ganglia as compared with those of a more advanced age. Removal of the hemispheres exerts less general functional disturbance in them than in those which have reached a greater degree of maturity, a fact of no small importance in relation to the progressive evolution of intelligence. But even in adult rabbits the lower centres rapidly regain their power of independent action, after the first shock caused by the removal of the hemispheres has subsided.

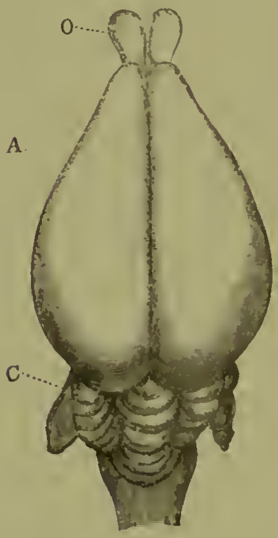


FIG. 14. — Brain of the Rabbit. A. The smooth cerebral hemisphere. O. The olfactory bulb. C. The cerebellum.

When the hemispheres have been removed from a rabbit (A, fig. 14) or guinea-pig, the animal, at first utterly prostrate, after a varying interval begins to show signs of the retention of a capacity for the performance of actions of a considerable degree of complexity. It is observable, in the first place, that the muscular power of the limbs has become enfeebled to a very considerable extent. The muscular weakness is proportionately much more marked in the fore than in the hind limbs. The animal can maintain its equilibrium on its legs, though of a rather unsteady character, and the fore paws have a tendency to sprawl, or to be planted in irregular positions. If the equilibrium is disturbed the animal is capable of regaining it. If the hind foot is pinched the animal will bound forward in the usual manner, until it strikes its head against some obstacle, or until the excitation has exhausted itself.

No one, as far as I am aware, has observed that power to avoid obstacles in the path manifested by frogs and fishes similarly treated.

The rabbit, therefore, continues its flight, once begun, in a headlong and blind manner. The pupils, however, still contract when a strong light is thrown into the eye, and the eyelids wink if the conjunctiva is directly menaced. A loud sound will cause the ear to twitch, and provoke a sudden start. Colocynth, or some other equally unpleasant sapid stimulus, will cause movements of the tongue and muscles of mastication in all respects resembling those characteristic of disgust, with efforts to get rid of the nauseous taste. Ammonia held before the nostrils will cause a sudden retraction of the head, or induce the animal to rub its nostrils with its paws.

Not merely does the animal respond by certain movements to a pinch or prick of its toes or tail, but if the pinch is a little more severe, it will respond with repeated and prolonged cries of that plaintive character with which all sportsmen are familiar who have gone hare or rabbit shooting. Vulpian specially calls attention to the plaintive character of these cries as distinguished from the brief cry which may be elicited when all the parts above the medulla have been destroyed. My own experiments entirely confirm the description which Vulpian has given of them. If the animal be left to itself, undisturbed by any form of external stimulus, it remains fixed and immovable on the same spot, and unless artificially fed, dies of starvation, like the frog, fish and bird, in the midst of plenty. If artificially fed, however, the animal may live an indefinite period.

With the exception of the greater degree of muscular paralysis and the diminished power of accommodation of movements in accordance with sensory impressions in general, and with visual impressions in particular, the phenomena manifested by rodents deprived of their cerebral hemispheres differ little from those already described in frogs, fishes and birds. The power of maintaining the equilibrium is retained, coordinated locomotive actions and emotional manifestations are capable of being excited by impressions on sensory nerves, essentially if not altogether to the same extent in all. In cats, dogs and higher animals, the prostration is so great, and there is such interference with motor power, that the independent activity of the lower centres, as far as relates to the maintenance of equilibrium and co-ordinated progression, practically ceases to exist; though the fact of emotional response to sensory impressions points to the conclusion that we have to deal, not with the complete absence, but only with the suspension of the other forms of functional activity. This conclusion is capable of substantiation by other facts, to be adduced when we come to consider in a more detailed manner the functions of the hemispheres.

§ 21. When we turn from the consideration of the facts themselves to the theory of their explanation, we enter on a *quæstio vexata* of physiology and psychology.

One fundamental fact, however, seems to be conclusively demonstrated by these experiments, viz., that in the absence of the cerebral hemispheres the lower centres, of themselves, are incapable of originating active manifestations of any kind. An animal with brain intact exhibits a varied spontaneity of action not, at least immediately, conditioned by present impressions on its organs of sense. When the hemispheres are removed, all the actions of the animal become the immediate and necessary response to the form and intensity of the stimulus communicated to its afferent nerves. Without such excitation from without the animal remains motionless and inert. It is true that some of the phenomena which have been described would seem to be opposed to this view, but they are so in appearance only and not in reality. Thus, we have seen that a frog may occasionally move its limbs spontaneously, and a bird may yawn, shake its feathers or change its foot; but these actions are the result of impressions arising from cutaneous irritation or internal discomfort —'ento-' or 'epi-peripherical' impressions—or in some cases from the irritation caused by the wounded surface resulting from the operation.

The same law satisfactorily accounts for the immobility of the frog on land, and the activity of the fish in the water. In the one case there is no external source of irritation, in the other the contact of the water with the body surface acts as a continual external stimulus to the natatory mechanism. As this is constant, so the fish continues to swim until arrested by some insurmountable obstacle or by pure nervous or muscular fatigue. We have only to throw the frog into the water to complete the proof. The frog, like the fish, will continue to swim until it reaches dry land or becomes exhausted. Hence the phenomena manifested by the different classes of animals after ablation of the hemispheres admit of generalisation under the law that the lower ganglia are centres of immediate responsive action only, as contradistinguished from the mediate or self-conditioned activity which the hemispheres alone possess.

We have next to inquire, What is the nature of the impression which is the immediate antecedent of this responsive activity? Is it a purely physical phenomenon, or has it likewise a subjective side? In other words, are these actions merely reflex or excito-motor, or are they the result of sensation properly so-called? If we define sensation as the consciousness of an impression, it will be seen that the problem to be solved is, whether consciousness is an accompaniment of the activity of these centres, and whether, therefore, we have here to deal with truly psychical phenomena. I have already, in discussing the functions of the spinal cord, observed that the existence or not of consciousness in others than ourselves, is entirely a matter of inference or testimony. In the lower animals we can only judge from the character of the phenomena they manifest, and by analogy with our own actions. If it is difficult to determine the nature of the adaptive faculty of the spinal cord, it is not the less difficult in regard to the centres now under consideration. If we adopt the metaphysical view, that mind and consciousness form an indivisible unity, and that annihilation of one great class of mental manifestations necessarily involves the annihilation of mind as a whole, seeing that the indivisible cannot be divided, it would be easy to argue that, as the ablation of the hemispheres abolishes certain fundamental powers of mind, therefore the functions of the lower centres must be outside the sphere of mind proper. But this way of looking at the subject will not harmonise with the facts of physiology, for, as we shall find when we come to discuss the functions of the hemispheres, whole tracts may be completely and irrevocably cut out of the territory of intellectual consciousness without interfering with the integrity of consciousness *quâ* others; and will may be abolished, while consciousness remains. Hence we are not entitled to say that mind, as a unity, has a local habitation in any one part of the encephalon, but rather that mental manifestations in their entirety depend on the conjoint action of several parts, the functions of which are capable, within certain limits, of being individually differentiated from each other. If we have regard merely to the character of the reactions which result from impressions made on the various organs of sense, it will be found impossible to distinguish between them, and those which are actuated by a distinct consciousness of the impression. Thus, a severe pinch on the tail or foot of a brainless rabbit elicits not merely convulsive reflex movements, such as may result from the activity of the spinal cord alone, but calls forth the repeated and prolonged cry which is characteristic of pain. The frog, in like manner, would appear to have a distinct sense of pain when it makes frantic efforts to escape from its hot bath. And it would seem to be a consciousness of retinal impressions which causes the frog, when urged to move, to leap aside so as to avoid an obstacle placed in its path; or which causes the fish, under similar circumstances, to deviate sharply from the straight course which it would otherwise pursue. But we cannot rely on appearances alone. For, on the other hand, it may be that the mesencephale is a centre of reflex reaction of a special form, differing from the spinal cord not in kind, but only in degree of complexity. Just as the medulla oblongata is a centre of more complex and special co-ordination than the spinal cord, so the mesencephale may be the centre of still more complex special reflex actions, among which may be the reflex expression of emotion. Hence the plaintive cry elicited by pinching the foot of a rabbit may be merely a reflex phenomenon, not depending on any true sense of pain. And so the leap to the side which the brainless frog makes so as to avoid an obstacle, would be merely the resultant of two simultaneous impressions, the one on its foot and the other on its retina. Lotze ('Göttingische Gelehrte Anzeigen,' 1853, quoted by Goltz, *op. cit.*), also argues that even though such apparently intelligent reactions should not be conditioned by the primary constitution of these nerve centres, they may be the result of an organic nexus established between certain impressions and certain actions by the past experience of the animal under similar circumstances; that which was primarily a conscious action, becoming by frequent repetition a reflex action of a secondary character. Of this conversion of conscious action into secondary reflex, numerous other examples might be quoted. This view, however, will not of itself suffice to account for all the phenomena.

By a series of ingeniously contrived experiments, Goltz has shown that, even when the limbs of a frog were so fixed or placed in positions which could never have occurred in its past experience, the animal, without its hemispheres, retained the power of adapting its movements in accordance with these unusual and abnormal conditions. This would indicate that if these centres are centres merely of reflex action, the reaction is that of a machine possessing in some way the power of self-adjustment.

But the mere faculty of adaptation is not necessarily a proof of consciousness, for, as we have seen, it exists in some degree in the spinal cord, and if it is not regarded as proof of conscious action on the part of the cord, neither can it be taken as such here; for it may be that the more complex adaptation manifested by the mesencephale is simply the result of more complex and special afferent and efferent relations. On this supposition we might account for the difference which is observed in the behaviour of two frogs, the one retaining its mesencephale and cerebellum, the other only its cord, when placed together in a vessel of water, the temperature of which is gradually raised. The mechanism of leaping possessed by the one may be set in action by a stimulus which is not sufficient to excite convulsive reaction through the spinal cord of the other. And that this may be so, is rendered more probable by another important fact observed by Goltz, viz., that the reflex movements of the limbs of the decapitated frog can be excited in the usual manner (*e.g.* by chemical irritation) during the continuance of the heat which is already causing the other to make efforts to escape. We cannot, therefore, rely on the phenomena of adaptation as indisputable proof of the existence of consciousness. Carpenter, who with Longet regards the mesencephale as the *sensorium commune* or seat of sensation, and terms the reaction of these centres *sensori-motor* reaction, adduces in support of the existence of consciousness the evidently conscious actions of invertebrate animals, which have no true cerebral hemispheres, but only a series of ganglia homologous with the mesencephalic ganglia of vertebrates.

This would be a powerful argument if the cases were in other respects quite parallel. But it is materially weakened by the fact that invertebrate animals are capable of actions of an entirely *different kind* from those of vertebrates deprived of their cerebral hemispheres.

These animals manifest a varied spontaneity of action under, as far as we can see, the same external conditions; they seek their food, are capable of education, and learn to adapt their actions so as to seek what is pleasant and avoid that which is painful; faculties which are entirely abolished by removal of the cerebral hemispheres in vertebrates.

From this I would argue, that the ganglia of the invertebrates are not completely homologous with the mesencephalic ganglia of vertebrates, for if they were so, we should expect that not merely sensation, but also the other psychical faculties, should be manifested by vertebrates deprived of their cerebral hemispheres, even though to a less degree. But it is not a difference in degree only which is observed, but a manifest difference in kind. It is probable, therefore, that in the ganglia of the invertebrates there are nerve cells which perform, in however lowly a manner, the functions of the cerebral hemispheres in vertebrates. The fact of consciousness being correlated with the activity of the mesencephale still, therefore, as far as relates to experiments on the lower animals, remains undecided. It is more easy to ascertain the conditions of consciousness in ourselves. The only proof of consciousness of an impression, except for the immediate present, is the fact that we remember it. Without some degree of persistence in memory, sensation practically has no psychical import; without memory to serve as a basis of comparison between past and present there can be no perception, and no rational or intelligent action founded on impressions received by our organs of sense. It is usual to regard the hemispheres as the seat of memory and perception, but the question still remains whether the hemispheres are necessary for sensation or consciousness of impressions of the moment.

We obviously cannot obtain any answer to the question, when the functions of the hemispheres are so affected as to prevent the expression in words or by gesture language of subjective states, if any such really exist. But we have experiments of disease which practically detach the hemispheres from their mesencephalic connections, and leave thought and speech intact, so that we can obtain direct testimony as regards the consciousness of impressions. Such an experiment is performed by a lesion of the crus cerebri or of the posterior part of the peduncular expansion (see § 68), phenomena not unfrequently occurring in clinical experience. When this occurs, the individual has absolutely no consciousness of tactile impressions made on the opposite side of his body, *however much he may strain his attention to receive them.* In the mesencephale alone, therefore, sensory impressions are not correlated with modifications of consciousness; whence we must conclude that sensation is a function of the higher centres. The results of experiments on monkeys, to be subsequently detailed, are quite in accordance with those of disease in man. We have reason to believe, from the homology of the mesencephale of man to the lower vertebrates, that the functions are of the same type, and only differ in degree of independence, and therefore I would refuse the term sensation, in its acceptation as the consciousness of an impression, to the receptivity of the mesencephalic centres. But how are we to designate this self-adjustable respondence to sensory impressions? Flourens, with whom I agree, was of opinion that sensation proper was abolished by removal of the cerebral hemispheres. Vulpian qualifies the term sensation, ascribed to the mesencephale by Longet and Carpenter, by the adjective '*crude*' or '*obscure*,' in contradistinction to the '*distinct*' sensation or '*perception*,' as he terms it, of the cerebral hemispheres. Goltz, without deciding the question positively, in one way or the other, ascribes to the mesencephale an '*adaptive faculty*' (Anpassungsvermögen), and terms the reactions of these centres '*responsive movements*' (Antwortsbewegungen), terms which I have adopted and frequently employed. Huxley would call a sensory modification which is not correlated with consciousness a *neurosis*, and one which has also a subjective aspect a *psychosis*, terms which might be employed, but for the disadvantage of neurosis being used in medicine to signify a diseased function of nerve. If we avoid the term sensation altogether, and arbitrarily use the term *æsthesis* to signify a mere physical impression on the centres of special sense, and the term *noesis* to signify a conscious impression, we may avoid some of the difficulties caused by the ambiguities involved in the common terms. The reaction of the mesencephalic and cerebellar centres might be termed *æsthetiko-kinetic*, and be thus distinguished from the *kentro-kinetic* or excito-motor action of the spinal cord on the one hand, and the *noetiko-kinetic* action of the cerebral hemispheres on the other (see Chapter XII.).

Having thus far considered the general character of the functions of the mesencephale and cerebellum apart from the cerebral hemispheres, we have next to inquire more specially into the individual forms of functional activity, with the view, if possible, of determining the mechanism and central localisation of each.

We may classify the functional manifestations already described under three heads:—1. The function of equilibration, or maintenance of the bodily equilibrium. 2. Co-ordination of locomotion. 3. Emotional expression. The first and second of these are so intimately bound up together, that the consideration of the one implies, more or less, the consideration of the other.

I. The Maintenance of Equilibrium.

§ 22. That this is a function of the mesencephalic and cerebellar centres is clearly demonstrated by Goltz's balancing experiments on frogs and birds, already described. It has been seen that an animal, deprived of its cerebral hemispheres, is capable not only of maintaining its equilibrium, if undisturbed, but of regaining it when overthrown. It can incline the head and body in such a manner, when the basis of support is tilted, as to keep the centre of gravity within the base.

Considerable diversity and complexity of muscular movements, all adapted for this purpose, are called into play, according to the conditions under which the animal may be placed. A frog placed on an inclined plane of steep gradient, is impelled, as it were, irresistibly to climb up, in order to prevent itself falling backwards. A pigeon accidentally stepping off the table into thin air is irresistibly urged to flap its wings, to sustain itself until it regains *terra firma.* Mammals, deprived of their cerebral hemispheres, retain the same power, though to a less marked extent; the various orders of animals differing much in this respect.

The maintenance of the equilibrium is an example of æsthetiko-kinesis, and involves the conjoint operation of three separate factors:—1. A system of afferent nerves. 2. A co-ordinating centre. 3. Efferent tracts in connection with the muscular apparatus concerned in the action. The faculty of equilibration is overthrown by lesions of the afferent apparatus alone, or by lesions of the encephalic centre alone, or by lesions of the efferent tracts alone, or by conjoint lesion of all. Various degrees and forms of perturbation of this function will result, according to the nature and extent and position of the lesion. In many respects the maintenance of the equilibrium resembles the tone of muscles. Lesions of the afferent nerves, central ganglia, or motor nerves destroy the tone of muscles; and, according as this occurs in both or only in one group of antagonistic muscles, we have complete muscular flaccidity or flexor or lateral distortion. So, in regard to equilibrium, similar lesions may cause complete overthrow, or various forms of distortion exhibited as reeling, staggering, rotation, and the like.

The afferent apparatus is of a compound nature, but mainly consists of three great systems, which, in conjunction, form that synæsthesis on which the due maintenance of equilibrium and co-ordination depend. The equilibrium is disturbed by lesions of one or more, or all, of these. These three systems are—1. Organs of reception and transmission of tactile impressions. 2. Organs for the reception and transmission of visual impressions. 3. The semicircular canals of the internal ear, and their afferent nerves.

The influence of tactile impressions.

§ 23. That these form an integral factor in the general consensus is demonstrated, both by direct experiment and by the facts of pathology.

We have already seen that a frog, deprived of its cerebral hemispheres, but in which the optic lobes and cerebellum are intact, still retains the power of maintaining its equilibrium and adapting its movements to this end, under diverse conditions. If, now, the skin be removed from the hinder extremities, the animal at once loses this power, and falls like a log when the basis of support is tilted. The removal of the skin has destroyed the receptive organs of those sensory impressions which are necessary to excite the co-ordinating centre to the adjusted combinations of muscular action requisite for equilibration.

The sensory nerves of the denuded surface are not of themselves capable of conveying the proper stimulus to the co-ordinating centre. This is a fact in harmony with the law laid down by Volkmann, and confirmed by all subsequent observers, that reflex reactions are more capable of being excited by impressions on the *cutaneous* extremities of afferent nerves, than by stimuli applied to any other part of their course. The pathological evidence of the influence of tactile impressions on the functional activity of the centres of equilibrium and co-ordination is furnished by the phenomena of the disease known as locomotor-ataxy. In this disease the individual complains of a numbness in the lower extremities, chiefly in the soles of the feet, with diminished or entire absence of sensibility to tactile impressions, so that he feels as if he were standing on soft velvet or in air. Other forms of sensibility, however, may remain unaffected, such as to painful stimuli or to temperature. A cold iron laid against the feet causes a sensation of cold, but not of a cold *something*. The patient so affected retains his voluntary motor power, and can move his legs freely and forcibly so long as he is in the recumbent posture. When, however, he attempts to stand or walk, he plants his feet irregularly, and staggers or falls. This inability to maintain the equilibrium is best seen when the patient tries to stand with the feet parallel to each other and heels and toes approximated. He sways and oscillates in an alarming manner, and may fall if unsupported.

The disturbance of equilibration and co-ordination is greatly intensified if the patient shuts his eyes or attempts to stand or walk in the dark. Under such circumstances, in fact, both station and locomotion become impossible.

Here we have an instance of disturbance of the general consensus, which, however, is partly compensated for by voluntary adaptation and by the other afferent factors, viz., the visual and the auditory (labyrinthine) impressions. The exclusion of the visual impressions, as when the eyes are shut, or when the patient is in the dark, renders the perturbation of function complete. This disease, which was first indicated by the late Dr. Todd, but first clearly differentiated by Duchenne, is found to depend on degeneration (sclerosis) of the posterior columns of the spinal cord and the posterior roots of the spinal nerves. We need not stay here to discuss whether the morbid process interrupts the path of tactile impressions (Schiff, Sanders-Ezn), or whether the inco-ordination is due to the affection of commissural systems of fibres connecting and co-ordinating the various segments of the cord and their posterior roots (Todd, Ludwig and Woroschiloff).

The fact of chief importance with which we have to deal, is that the loss of the faculty of equilibration and co-ordinated progression proceeds *pari passu* with the diminution of sensibility to certain forms of cutaneous impressions. These are especially impressions of contact, and it would seem that the contact of the soles of the feet with the ground is in great measure the exciting cause of the co-ordinated combination of muscular actions concerned in the maintenance of the upright posture and steady progression. The condition is analogous to that of the frog whose hinder extremities have been flayed. Impressions can still be conveyed from the denuded surface, but they are not of that character adapted to call forth the regulated functional activity of the encephalic centres which we are considering.

The fact that equilibration and co-ordinated locomotion are possible in the entire absence of the hemispheres, and therefore of true sensation, indicates that these functions do not require the intervention of consciousness. In the presence of the hemispheres, however, the same impressions which excite the adaptive activity of the mesencephale and cerebellum, travelling onwards also excite modifications of consciousness if the attention is directed to them. But they go on equally well, if not better, when consciousness is concentrated on some other object. The possible correlation of consciousness, however, when the hemispheres are retained, as in locomotor ataxy, complicates the question as to the independent action of the mesencephale; and it is only by the analogy of the lower animals that we can exclude consciousness as an essential factor. But while consciousness need not be excited in the normal condition, it is certain that abnormal conditions, such as those observed in locomotor ataxy, manifest themselves in consciousness in a painful degree, as vertigo, etc., and to this, in great measure, are due the attempts to compensate for the disorder of a self-adjusting mechanism by voluntary efforts at adaptation. These may succeed, to a great extent, in overcoming a degree of derangement such as would render an animal deprived of its hemispheres utterly helpless.

It is held by some that the special cause of the symptoms observed in locomotor ataxy is a loss of what is termed the 'muscular sense.' By this is meant a consciousness of the state of contraction and force exerted by the muscles. According to this view, it is to the loss of this sense that the inco-ordination in locomotor ataxy is due.

If the cases of the ataxic frog and ataxic patient were quite parallel we should at once dispose of this theory, as it is merely an abolition of the receptivity to cutaneous impressions which causes the loss of equilibration in the former. But we may not assume, without further inquiry, that an exact parallelism holds. If the loss of the muscular sense be taken to signify the loss of *consciousness* of muscular action, I should, on the grounds already given for excluding consciousness altogether from parts below the hemispheres, reject this hypothesis as an explanation of the ataxia. But it is possible that the muscles, like the organs of special sense, may be the seat of origin of afferent impressions, which are transmitted with the others, to the mesencephalic or cerebellar centres. The question is, whether we have sufficient grounds for assuming the existence of such special muscular impressions. It is undoubtedly true, as E. Weber established, that we are able to discriminate between weights beyond the limits of mere sensations of pressure on the skin, by the degree of muscular contraction necessary to raise or sustain them. But we have here to deal with a complex result, for in addition to any special impressions originating in the muscles, we have impressions caused by cutaneous contact and pressure, muscular displacement, tension of ligaments, and, if the weight is heavy, general bodily strain. That these enter largely into the composition of what is termed the muscular sense is generally admitted. It was established by Schroeder van der Kolk, that when a mixed nerve sends motor branches to a muscle it sends sensory fibres to the overlying skin. This distribution of nerves would account for the origin of impressions resulting from the displacement of the muscle during contraction. The joints, ligaments and periosteum are also supplied with sensory nerves and with Pacinian corpuscles (Rauber), organs which are specially adapted to receive stimulation by mechanical pressure. In these, therefore, we have the possible origin of further impressions caused by the strain of supporting a weight. But beyond these, have we any proof of inherent sensibility of the muscles which may contribute to the general result? This question has been much discussed, and many physiologists have entirely denied the presence of sensory nerves in muscles, but on very insufficient grounds. Muscles are comparatively insensible to certain forms of irritation, which act powerfully on cutaneous surfaces, such as section, mechanical or chemical irritation, but they are distinctly sensible to others. Muscles are the seat of the sensation of fatigue, which is apparently due to the accumulation of the waste products of their activity. Furthermore, as Duchenne has shown, muscles are distinctly sensible to electrisation, which causes a peculiar vibratory thrill quite independent of cutaneous impressions, for it can be felt in muscles denuded of their cutaneous covering.

Besides these forms of sensibility, muscles are the seat of the acutely painful sensations of cramp. The sensation of cramp has been attributed merely to the compression of sensory nerves passing through them, and not to a neurosis of sensory nerves of their own. This, however, does not afford a satisfactory explanation of the facts. Vulpian shows that contractions in every sense as powerful as those characteristic of cramp may be caused without the painful sensation of cramp, such as ought to be experienced if it were in reality due to mechanical pressure on transcurrent or adjacent sensory nerves. These facts render it probable that the muscles receive special sensory nerves, and that it is to a neurosis of these nerves that both the pain and the tetanic contraction characteristic of cramp are due. That the muscles do, in fact, receive sensory nerves has been demonstrated by the recent researches of Sachs ('Centralblatt für die Med. Wissensch.' 1873). They are derived from the posterior roots of the spinal nerves, and have a course and distribution distinct from those of the motor nerves. Rauber ('Centralblatt für die Med. Wissensch.' 1867) has also shown that Pacinian corpuscles are to be found in the fasciæ of the muscles; and that when the nerves to which these are attached are divided, a condition resembling ataxy results. Whether the sensory nerves of the muscles are of themselves capable of conveying the impressions generated by muscular contraction, we have no means of deciding absolutely; but the peculiar vibratory thrill excited by electrisation seems to argue powerfully in favour of the fact that they form at least part of the complex result.

As a general rule, diminution of tactile sensibility coincides with impairment of the muscular sense. But there are certainly cases in which the impairment of tactile sensibility does not proceed *pari passu* with the impairment of muscular sense. These peculiarities in the conduction of different classes of impressions are not quite satisfactorily accounted for; but on the other hand, there are no pathological instances of abolition of the muscular sense without greater or less impairment of tactile sensibility. The facts of pathology and experiment tend in the opposite direction. When the posterior roots of the spinal nerves are cut, as in Bernard's experiments, the phenomena are such as would coincide with abolition of muscular sense. In pathological cases, in which tactile sensibility is entirely abolished, the muscular sense is also abolished. A condition resembling motor paralysis results, though the power of movement is not in reality destroyed, for the limbs may be moved under the guidance of the eye, though all sense of movement is quite annihilated. This is a condition not unfrequently seen in what is termed cerebral hemianæsthesia (see § 68), and it is a well-known fact that one of the branches of the fifth nerve was at one time taken as a motor nerve, when in reality the immobility which followed its division was due to the paralysis of sensation only.

Still further, morbid anatomy demonstrates that in cases of locomotor ataxy, when the muscular sense has been lost, the anterior roots of the spinal nerves, which Brown-Sequard is inclined to regard as subserving this function, are entirely free from discoverable lesion. These data seem conclusively to prove that it is through the posterior roots and afferent tracts that the impressions caused by muscular action are conveyed.

Whether we have a consciousness of muscular effort apart from the fact of muscular action, as Bain assumes, is a question which will be discussed in a subsequent chapter (Chap. IX. § 75).

We have no good grounds for ascribing the inco-ordination of locomotor ataxy to loss of the muscular sense in particular, for ataxy frequently exists without any marked impairment of this faculty (Leyden, 'Muskelsinn und Ataxie,' Virchow's Archiv, xlvii.). Nor, on the other hand, can it be said that the ataxy depends on loss of cutaneous sensibility in general. In locomotor ataxy differences of temperature can be perceived, and pain may be felt on the application of mechanical stimuli of a certain degree of intensity. Hence it would appear that it is not any and every form of tactile impression that is the efficient excitant of the co-ordinating centres of equilibrium and locomotion, but a special form of cutaneous impression generated by contact.

In those cases, generally of an hysteric nature, in which there may be loss of cutaneous sensibility without ataxy, the real causation of the loss of sensation, or of sensory perception, depends on organic or functional affection of the higher encephalic centres, above those concerned in the co-ordination of movements independently of conscious activity. A lesion of the afferent tracts below the mesencephale must interrupt the path of impressions necessary to excite the normal action of the mesencephalic co-ordinating centres, as well as cause anæsthesia; but a lesion above the mesencephalic and cerebellar centres might cause anæsthesia without producing ataxy, inasmuch as these centres would still be in normal relation with those afferent tracts which are an essential part of the mechanism.

Just as special forms of reflex action are excited by special stimuli in the case of the decapitated frog, so it would appear that the mesencephalic and cerebellar centres require a special kind of tactile impression to call them into appropriate action.

Whether we assume, with Brown-Sequard, that the different forms of tactile impressions are conveyed by different nerves, or with Vulpian, that the different forms of impression are conditioned by the nature of the stimulus applied to the peripherical terminations of common afferent nerves, we may equally admit the possibility of lesions affecting the transmission of one set of impressions and leaving others comparatively unimpaired. That the lesions found in locomotor ataxy do affect principally the transmission of impressions of contact is abundantly proved by the clinical history of the disease; and that the posterior columns of the spinal cord are in some measure concerned in the conveyance of such impressions is confirmed by the experiments of Schiff and Sanders-Ezn. It is extremely difficult to determine this question in the lower animals, for though reactions to certain forms of tactile impression may still continue to be manifested by animals in which the posterior columns of the cord have been divided, this does not invalidate the view which attributes special functions to the posterior columns in relation to the conveyance of impressions of that nature, which call into play the co-ordinating centres of equilibrium and locomotion.

From the phenomena observed in the flayed frog, as well as from those of locomotor ataxy, we find, therefore, that tactile impressions form an integral factor in the synæsthetic combination on which the due co-ordination of equilibrium and locomotion depends.

The influence of visual impressions.

§ 24. Equilibration and co-ordination of movements are not necessarily dependent on these, for the tactile and labyrinthine impressions are of themselves sufficient to maintain the due functional activity of the encephalic centres. They, however, exert an important influence, and they may in a measure compensate for the loss of tactile impressions. We have seen that in locomotor ataxy equilibration and co-ordination are not altogether impossible, notwithstanding the default of tactile impressions, so long as visual impressions continue. When these are shut out by closure of the eyes, or by negation of light, the mechanism of the encephalic centres is completely deranged. In the attempts at compensation, it cannot be doubted that voluntary efforts largely enter, but in this case the centres of sensation and volition are brought into action. But conscious efforts, except under the guiding influence of present visual impressions, are entirely unable, of themselves, to compensate for the loss of the tactile impressions. In this we see the necessity of immediate, in contradistinction to mediate, or cerebral registrations of, visual impressions, for the due excitation of the co-ordinating centres, a fact which shows the mainly æsthetiko-kinetic nature of the phenomena. Some facts of experiment are on record, which tend to show that direct disturbance of the function of equilibration may result from interference with the organs of vision, notwithstanding the normal existence of tactile and labyrinthine impressions. Longet found that sudden destruction of one eye of a pigeon caused the animal to spin for some time round a vertical axis. This has been explained away by Vulpian and others as merely the result of the dread of obscurity on the one side, and the desire the animal exhibits to keep its eye on both sides; and hence its voluntary rotation. This does not seem to me an adequate explanation of the phenomena. It is, I think, more probable that the rotation is a unilateral distortion consequent on the sudden interference with a usually double visual impression; a functional disturbance which, however, rapidly subsides. This functional derangement of the co-ordinating centres rises into consciousness as vertigo, this being merely the subjective side of the physical disorder of a self-adjusting or æsthetiko-kinetic mechanism. The vertigo of consciousness, however, may, secondarily, bring volitional efforts to bear, either to compensate for the tendency to distortion by other antagonistic muscular action, or to inhibit the reflex tendency altogether. To one or other of these various causes the cessation of the primary disturbance of equilibrium, consequent on interference with the normal conditions of vision may be ascribed.

The influence of visual impressions on the faculty of equilibration, is further forcibly illustrated in the disturbances of equilibrium consequent on their perversion resulting from paralysis of a purely peripherical origin of certain ocular muscles. The giddiness which accompanies nystagmus, or spasmodic oscillation of the eyeballs, may or may not be of a peripherical origin, but when the external rectus becomes paralysed by affection of the sixth nerve, or in cases of oculo-motor paralysis from disease of the third nerve, one of the characteristic symptoms is the giddiness or reeling which comes on when the patient attempts to walk steadily in a given direction with the healthy eye shut. The abnormal conditions of the organs of vision cause a disharmony of co-ordination, accompanied with a subjective feeling of vertigo.

Though equilibration and co-ordination of locomotion are possible, independently of visual impressions, they are not carried out with the same degree of precision or steadiness, a fact which is exemplified in the uncertain and wavering character of the motor adjustments, even of the most habitual or. automatic character, when the eyes are shut or the light absolutely withdrawn.

The influence of labyrinthine impressions.

§ 25. These are the most important of all in relation to the due maintenance of equilibrium. This fact was first demonstrated by Flourens' remarkable experiments on the semicircular canals of pigeons.

The internal ear or labyrinth is imbedded in the petrous portion of the temporal bone, and consists of a central chamber called the *vestibule*, which communicates in front with the cochlea, and behind with the semicircular canals; on its outer aspect it opens towards the cavity of the tympanum or drum of the ear (fig. 15, A). The semicircular canals form three bony tubes which communicate with the vestibule by five apertures, two of the ends uniting into one (fig. 15, B, 7). The canals form each two-thirds of a circle, and at one end each presents a dilatation called the *ampulla*. The canals are termed, according to their position and relation to each other, the *superior vertical* (fig. 15, A, 4), the *posterior vertical* (fig. 15, A, 2), and the *horizontal* (fig. 15, A, 3). Within these bony tubes exist membranous canals (fig. 15, B), which have the same shape as the bony tubes, but are of less diameter, and are separated from the bony walls by a liquid called the *perilymph*. Each canal has a dilatation or ampulla situated in the corresponding dilatation of the bony canal, and all communicate with a common sinus situated in the vestibule and called the utricle (fig. 15, A, 5). These membranous canals are filled with liquid called the *endolymph*. On the ampullary dilatations of the membranous canals are distributed respectively three branches of the vestibular division of the auditory nerve (see fig. 15, B).

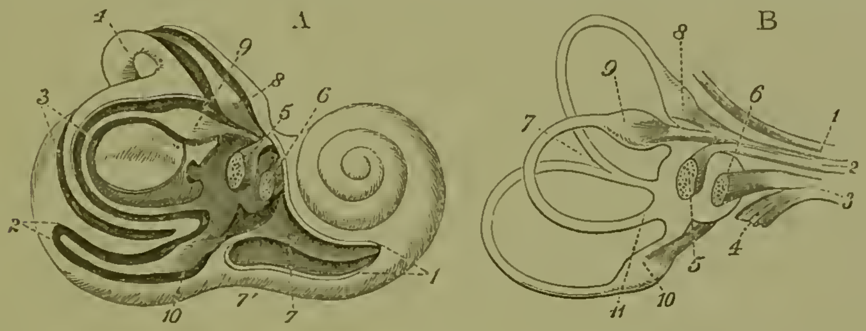


FIG. 15.—The Interior of the Right Labyrinth with its Membranous Canals and Nerves (Breschet). A. The outer wall of the bony labyrinth is removed so as to display the membranous parts within. 1. Commencement of the spiral tube of the cochlea. 2. Posterior semicircular canal, partly opened. 3. External or horizontal canal. 4. Superior canal. 5. Utriculus. 6. Sacculus. 7. Lamina spiralis. 7′. Scala tympani. 8. Ampulla of the superior membranous canal. 9. Ampulla of the horizontal. 10. Ampulla of the posterior semicircular canal.—B. Membranous labyrinth and nerves detached. 1. Facial nerve in the internal auditory meatus. 2. Anterior division of the auditory nerve giving branches to 5, 8 and 9, the utricle and the ampullæ of the superior and horizontal canals. 3. Posterior division of the auditory nerve, giving branches to the sacculus (6), and posterior ampulla (10), and cochlea (4). 7. United part of the superior and posterior canals. 11. Posterior extremity of the horizontal canal.

This intricate apparatus, besides being imbedded in bone, is of small size and not easily reached, but yet is capable of being exposed for exact experimentation, especially when the ingenious plan, proposed by Vulpian, is adopted, of feeding the animals with madder, which causes the canals to become stained of a bright red, in the midst of bony tissue of a paler hue.

When the membranous canals are divided, very remarkable disturbances of equilibrium ensue, which vary in character according to the seat of the lesion. When the horizontal canals are divided, rapid movements of the head from side to side, in a horizontal plane, take place, along with oscillation of the eyeballs, and the animal tends to spin round on a vertical axis.

When the posterior or inferior vertical canals are divided, the head is moved rapidly backwards and forwards, and the animal tends to execute a backward somersault, head over heels.

When the superior vertical canals are divided, the head is moved rapidly forwards and backwards, and the animal tends to execute a forward somersault, heels over head. Combined section of the various canals causes the most bizarre contortions of the head and body. Results similar to these, first observed by Flourens on pigeons, and confirmed by Vulpian and others, are also observed to follow injury of the semicircular canals in mammals, as was also shown by Flourens; and we have certain facts of disease (Menière's disease) which indicate that the same is true of man.

Pigeons in which the semicircular canals have been injured may be kept alive for an indefinite period, as both Flourens and Goltz ('Pflüger's Archiv für Physiologie,' 1870) have shown. When the semicircular canals on one side only have been injured, the animals ultimately recover the power of maintaining their normal attitude. If, however, they are injured on both sides, the animal never again recovers the power of holding itself erect and steady. The most strange attitudes are assumed. Goltz describes a pigeon so treated, which always kept its head with the occiput touching its breast, the vertex directed downwards, with the right eye looking left and the left looking to the right; the head being almost incessantly swung in this position in a pendulum-like manner. The agitation of the head subsides if the animal is allowed to rest quietly, but when it is disturbed, or when it attempts voluntarily to walk, the agitation becomes extreme. Frequently it is seized with sudden attacks as of vertigo, and staggers or falls. Flying is impossible. If the animal is thrown in the air, it makes useless flapping of its wings, but falls like a stone. It is utterly unable to adapt its movements to maintain its equilibrium, if the basis of support is shaken or tilted. The animal is able to eat and drink, but with great difficulty, on account of the abnormal position and agitation of its head and body.

How are these strange phenomena to be accounted for?

The first supposition which naturally suggests itself is that these phenomena are somehow consequent on disturbances of the sense of hearing, seeing that the injuries affect the mechanism of the ear. This, however, is not the case, for Flourens has shown that animals in which the semicircular canals have been injured still retain their sense of hearing, at least as far as regards aërial sound vibrations. When the cochlea alone was destroyed, the animal lost its sense of hearing, but did not lose the faculty of equilibration. Nor, on the other hand, can it be said that the disturbances of equilibrium are necessarily dependent on affection of conscious impressions of any kind, for Flourens found that similar results followed injury to the semicircular canals of pigeons from which he had some time previously removed the cerebral hemispheres. Vulpian, Brown-Sequard and others ascribe the phenomena to reflex motor disturbances, caused by irritation consequent on the mechanical injuries. This may suffice to account for some of the first effects of the lesion, but this is evidently not all, for, as Goltz observes, the phenomena continue long after the wounds have been entirely healed up. We must therefore seek for some more satisfactory explanation. That the disturbances are consequent on interference with or perversion of certain impressions which act on some central organ of co-ordination, is shown by the fact that section of the auditory nerve within the skull causes marked disturbances of equilibrium (Brown-Sequard). This has been also shown very conclusively in frogs by Goltz. When the auditory nerve has been divided on both sides in a frog, the animal loses the power of maintaining its equilibrium when submitted to the balancing experiment already described. If its leg be irritated it jumps as before, but instead of alighting on its feet, it falls on its back, or in some other irregular fashion, and rolls over and over, before it can regain its normal position. These effects might be ascribed to injury of some part of the brain, in the attempt to divide the auditory nerves within the skull. But this view is disposed of by the fact that when the portion of the skull which contains the internal ear is detached from the rest without interfering with the interior of the skull, similar results ensue. The bizarre position of the head in pigeons in which the semicircular canals have been injured, is not due to distortion caused by active muscular contraction, for when the head is set right, which can easily be done without resistance, the animal becomes quite steady, and may continue so with little support; for if the beak be immersed in food or drink, the animal may continue to eat or drink for a short time in the normal manner, and only returns to its old position when the head is withdrawn.

The explanation given by Goltz, and borne out by these facts, is that the semicircular canals constitute an organ which is the seat of origin of impressions necessary for the due maintenance of the equilibrium of the head, and with it of the body.

Without these labyrinthine impressions, optic and tactile impressions are of themselves unable to excite the harmonious activity of the centres of equilibration.

The exact nature and mechanism of the labyrinthine impressions in general, and of each semicircular canal in particular, have been the subject of careful investigation of late, among others by Goltz (*op. cit.*), Mach ('Sitzb. der K. Acad. der Wissen.,' 1873), Breuer ('Med. Jahrbücher,' Heft 1, 1874), and Crum-Brown ('Journal of Anatomy and Physiology,' May 1874).

The impressions seem to be essentially dependent on the degree and relative variations in pressure exerted by the endolymph upon the ampullary dilatations of the membranous canals on which the vestibular nerves are spread. In the stationary position of the head a statical equilibrium exists. With each variation in the position of the head the tension on the ampullæ will become altered; the tension being, by the law of liquids, greatest on the most dependent ampulla. Thus, if the head is inclined to the right side, the pressure of the fluid in the horizontal canals will become altered, the fluid flowing *from* the right ampulla, and therefore diminishing the pressure, and *to* the left ampulla, so that the pressure on the left ampulla will increase correspondingly. Inclination of the head to the right, therefore, causes increase of pressure on the left horizontal canal, and *vice versâ*. By these symmetrical plus and minus variations, the centres of co-ordination are excited to appropriate activity, and the equilibrium is maintained. When the conditions are perverted by lesions of the canals, disturbances of equilibrium are the necessary result, and these will vary according to the seat of the lesion and the set of impressions which it disturbs. It is by means of the variations in tension in the ampullæ of both sides that we are sensible, according to Crum-Brown, of the axis, rate and direction of rotation of the head and body, apart from impressions of sight or touch. If a person be placed on a revolving disc, with his eyes shut, he is still able to determine the sense and extent of the angle through which the body has been rotated. After rotation is kept up for a certain time, the rate gradually diminishes, and after a time all sense of rotation entirely disappears. If the rotation is stopped, the individual feels as if he were being whirled round in the opposite direction. If he open his eyes, the discord between his visual, tactile and labyrinthine impressions causes the subjective feeling of vertigo. These phenomena are accounted for by the fact that rotation in a plane perpendicular to any of the canals, causes the endolymph, on account of its inertia, to press in the reverse direction against the ampullary nerves. This gradually ceases when the movements of the liquid and the bony canals have been equalised, and so the rotation ceases to be felt. On stoppage of the revolution, however, the liquid continues to move on, and so an impression of rotation in the reverse direction is occasioned. This also ceases after a time, on account of friction, and the phenomena subside.

The mechanism of these impressions is thus described by Crum-Brown :—‘ Each canal has an ampulla at one end only, and there is thus a physical difference between rotation with the ampulla first, and rotation with the ampulla last; and we can easily suppose the action to be such that only one of these rotations (say that with the ampulla first, in which case, of course, there is a flow from the ampulla into the canal) will affect the nerve termination at all. One canal can therefore, on this supposition, be affected by and transmit the sensation of rotation *about one axis in one direction only*, and for complete perception of rotation in any direction about any axis *six* semicircular canals are required, in three pairs, each pair having its two canals parallel (or in the same plane), and with their ampullæ turned opposite ways. Each pair would thus be sensitive to any rotation about a line at right angles to its plane or planes, the one canal being influenced by rotation in the one direction, the other by rotation in the opposite direction' ('Journal of Anat. and Phys.,' 1874, p. 330). These conditions are fulfilled by the fact that the two horizontal canals are on the same plane, and the superior vertical canal on one side is on the same plane as the posterior vertical of the opposite side, and *vice versâ*. Thus, 'in each case, there is one canal (the exterior (horizontal)) in a plane at right angles to the mesial plane, and two other canals (the superior and the posterior) in planes equally inclined to the mesial plane.' This arrangement furnishes the necessary conditions for a bilateral symmetery of the two ears, with three axes, each of which has two oppositely turned canals at right angles to it. This mechanism furnishes a self-adjusting apparatus for the origination and conveyance of impressions, which through the encephalic co-ordinating centres excite the appropriate bodily movements necessary for maintaining the equilibrium in accordance with each position of the head. The mechanism does not necessarily imply the activity of consciousness, for, as we have seen, the cerebral hemispheres are not indispensable to the function of equilibration. In the presence of the cerebral hemispheres, however, any perversion of the labyrinthine impressions, or discord between them and the other afferent factors on which the equilibrium is likewise dependent, excites not merely physical inco-ordination, but also the subjective feeling which we call vertigo. The feeling of vertigo, again, may excite complication in the otherwise purely reflex or æsthetiko-kinetic mechanism, by calling into play inhibitory or compensatory voluntary action.

The influence of the labyrinthine impressions on equilibration is illustrated in human pathology by the facts of 'Menière's disease,' so called from its having first been described by Menière. This disease is characterised by sudden attacks of vertigo and sickness, generally preceded by or associated with ringing or pain in the ear. The symptoms have been found to depend on disease of the semicircular canals, and the facts of experiments on animals show that the phenomena are essentially alike. Besides the similitude in the vertiginous movements, the two cases further resemble each other in the fact of sickness, for Czermak ('Comptes Rendus,' 1860) found that injury to the semicircular canals in pigeons usually caused vomiting along with the other effects already described. (Further, *vide* § 45.)

§ 26. We have thus far considered the influence of tactile, optic and labyrinthine impressions on the functions of equilibration and co-ordination, and it has been shown that the influence of each is capable of experimental demonstration. Though these are apparently the main factors in the general synæsthesis, the possible participation of other afferent factors in the general result is not absolutely excluded. I am not, however, aware of any facts, either of pathology or of physiological experiment, which would tend to show that olfactory or gustatory impressions have any direct influence on the centres of co-ordination. But there appear to me grounds for attributing some influence to visceral impressions. It is well known that cats and other members of the family Felidæ, including animals which possess in a marked degree the faculty of equilibration, have in their mesentery relatively larger numbers of Pacinian corpuscles, which are specially adapted for transmitting pressure stimuli to the sensory or afferent centres. These are in all probability the source of impressions conditioned by the state of the viscera, by which the degree of muscular action is regulated in the sudden movements of translation of which these animals are capable. I do not know of any physiological experiments bearing directly on this question, nor is it one likely to be elucidated by experimental inquiry, owing to the numerous complications which would be encountered.

The following considerations, as indicating the influence of visceral impressions on the encephalic centres of equilibration, are therefore more of a hypothetical nature. A very frequent accompaniment of disturbance of equilibrium is a distressing sense of depression, with nausea or actual sickness. As above stated vomiting is a frequent accompaniment of the disturbances resulting from injury to the semicircular canals of pigeons. It is also frequently seen in the sudden attacks of Menière's disease. Further, vomiting is a very common symptom of disease of the cerebellum, the chief centre of equilibration. It would seem, therefore, not improbable that the viscera are in relation with the centres of equilibration, and that they mutually affect each other. This is supported by the phenomena of a distressing form of dyspepsia, characterised by sudden attacks of giddiness, described by Trousseau under the name of *vertigo a stomacho læso*, and in all probability due to abnormal impressions originating in the visceral nerves. Visceral irritation, whether causing vertigo or not, usually excites nausea and vomiting; and so, conversely, disturbances of the mechanism of equilibration, either from central disease or from reflex irritation propagated to the centres, such as would result from lesions of the semicircular canals, may manifest themselves, as reeling or staggering on the motor side, and as vomiting and its accompaniments on the visceral side. The relation between the viscera and the centres of equilibration is also exemplified in the phenomena of sea-sickness. The nausea and sickness may be partly the visceral expression of disturbance of equilibration, but as sea-sickness may come on in the recumbent or sitting posture, and when the eyes are shut, the sickness and vertigo may, I think, with more probability be ascribed mainly to a perversion of the normal conditions of weight in the viscera, resulting from the repeated and irregular rising and falling of the basis of support. A condition resembling sea-sickness may in fact be produced in animals by mere mechanical disturbance of the stomach and intestines.

These considerations tend to establish a relation between the viscera and the centres of equilibration, in addition to those experimentally demonstrated in the case of tactile, visual and labyrinthine impressions. The subject is one, however, requiring further investigation.

II. Co-ordination of Locomotion.

§ 27. Animals deprived of their cerebral hemispheres, besides being able to maintain their equilibrium, are also capable of locomotion in their usual manner. Fishes balance themselves with their fins, and by alternate lateral strokes of the tail, swim forward with the same precision as before; frogs leap on land, or swim when thrown into the water; birds, if urged, walk forward, or fly if thrown into the air; rabbits bound away in their characteristic mode of progression, in response to appropriate external stimuli.

For reasons above stated (p. 40) it is impossible, in the higher animals, to demonstrate, experimentally, the retention of the faculty of co-ordinated locomotion in the centres situated below the hemispheres, but we are able to arrive at the same conclusion in another way. It is a fact of every-day observation, that the function of locomotion, once set into action, is carried on with all regularity and precision, without attention and apparently without consciousness, while the cerebral hemispheres are practically detached and engaged in other directions. From the homology subsisting between the mesencephalic and cerebellar centres of man and the lower vertebrates, we argue the homology of function, and what we have seen to be true of the lower animals, is to be regarded as more or less true of man. It may be, but we have no means of determining with exactitude, that this function is, in the lower animals, primarily or hereditarily inherent in the constitution of their nerve centres, and that in the higher it is rather, as Dr. Carpenter expresses it, a secondary reflex or automatic action, *i.e.*, the result of previous experience and conscious action. Whichever way we look at it, the result is the same, *viz.*, that whether primarily or secondarily developed, the co-ordination of movements of locomotion is a function of the lower encephalic centres.

It is manifestly impossible to draw a hard and fast line between the functions of equilibration and of locomotor co-ordination, for without equilibration locomotion becomes impracticable, and the same afferent factors are concerned in both.

In discussing the function of equilibration, I have frequently spoken of the two together ; but, theoretically, the two functions are capable of differentiation from each other. We can conceive an animal possessed of the power of maintaining its bodily equilibrium, and of the necessary muscular adjustments to this end *in loco*, but unable to move out of its position. Therefore, even though we may not be able to separate them practically, or localise the two functions in clearly differentiated encephalic centres, it is convenient to consider them apart.

The mechanism of co-ordinated locomotion, like the mechanism of equilibration, consists of—1, an afferent system of nerves ; 2, an encephalic co-ordinating centre ; 3, an efferent or motor system, by which the centre is brought into relation with the muscles of the trunk and limbs.

The afferent impulse, or that which excites the centre to action, in the first instance, may be various. In the animal deprived of its hemispheres, it can only come from without, and is generally some form of tactile stimulus.

The central apparatus of locomotion, once set into activity, continues to functionate (to use a convenient expression) in a rhythmical manner. The duration of this activity coincides with the degree of intensity or continuance of the primary stimulus, and the vitality of the nervo-muscular apparatus.

The fish in the water is under continual stimulation of its body surface by contact with the water, and, therefore, it continues to swim till arrested by some obstacle, or by fatigue. The rhythmical strokes of the tail would appear to be in a great measure conditioned by each other, the one stroke exciting the opposing stroke in regular succession. So the frog, when thrown into the water, is impelled to swim by the same kind of stimulus which acts on the body of the fish. The leaping movements on land are kept up in rhythmical succession by the successive impressions of contact with the ground after each leap. The pigeon makes bilateral rhythmical movements of the wings; quadrupeds either leap or walk—in the latter case usually with diagonally co-ordinated action of the fore and hind limbs; while man progresses principally by alternate pendulum-like swings of the lower extremities; the rhythmical succession being kept up by the alternate impressions of contact with the ground, which the sole of the foot receives after each step. Though in man the upper extremities have become differentiated away from purely locomotive purposes, yet it may be observed that they are co-ordinated with the lower extremities in the same diagonal manner as in quadrupeds; the right hand swinging with the left leg, and *vice versâ*. The upper extremities are likewise co-ordinated with the other bodily movements, in the adjustments necessary to the maintenance of equilibrium.

The necessity of rhythmical tactile impressions in the co-ordination of locomotion is shown in locomotor ataxy, a disease in which, owing to the loss or impairment of tactile sensibility, there is also difficulty in maintaining the equilibrium. The two functions are conjointly affected by lesion of the afferent factor common to both. Co-ordination of locomotion is also guided by the eye; and to some extent visual impressions compensate for the loss or impairment of the tactile impressions. Hence the necessity of sight in the locomotion of the ataxic patient. Except for purposes of locomotion the motor power of the ataxic individual is unimpaired, as shown by the complete voluntary control over the limbs in the recumbent posture.

III. Emotional Expression.

§ 28. The third class of functions manifested by animals deprived of their cerebral hemispheres, is that of certain forms of emotional manifestation usually spoken of as instinctive or reflex.

These are exhibited by man and animals under absolutely normal conditions. The expression follows the sensory impression so immediately and without conscious deliberation, that the æsthesis and its outward expression manifest themselves in consciousness at one and the same moment. We may feign emotion by voluntary effort, and we may, to a certain extent, inhibit emotional expression, but in the great majority of cases, the æsthesis manifests itself outwardly, in spite of all our endeavours to prevent it. The centre of these forms of emotional expression is evidently, therefore, below the region of conscious activity and ideation, and must have direct connection with the afferent nerves, which convey impressions of various forms and in various degrees of intensity; besides higher relations with the regions of conscious feelings.

The forms of emotional expression with which we are familiar, as resulting from peripheral sensory stimulation in animals subjected to physiological experimentation, are chiefly cries of various kinds, such as we would characterise, from our own experience or analogy, as expressive either of pleasure or pain; along with certain bodily movements, resembling those manifested under the influence of alarm or fear.

These are capable of being elicited in animals deprived of their cerebral hemispheres. I have already alluded (§ 17) to the remarkable fact, ascertained by Goltz, that frogs deprived of their cerebral hemispheres, can be made to croak readily and uniformly, when their back is gently stroked. The utterance of the sound is caused by stimulation of the cutaneous nerves of the dorsal region. If these nerves are cut, or the skin removed, the phenomena can no longer be excited; and the croaking likewise ceases, or is inhibited, if, at the same time, an impression is simultaneously made on another sensory nerve. Frogs express pleasure and satisfaction by croaking, and we regard the batrachian chorus, which may be heard on some warm summer evening, as a sign 'that it is well with the inhabitants of the marsh. The chorus ceases when a stone is thrown into the water' (Goltz). By reflex stimulation the same apparatus is set in action which the animal employs to give utterance to its conscious pleasure; and by other impressions the action is inhibited.

It has been stated by Voit that pigeons deprived of their hemispheres may still express sexual feelings by cooing, but there is reason to believe that Voit had not really entirely removed all above the mesencephale. The conditions of physiological experimentation are more likely to call forth the outward expression of painful states of consciousness. The fact has already been alluded to, that in rabbits deprived of their hemispheres, severe irritation of cutaneous nerves, such as of the foot, tail, or ear frequently elicits repeated and prolonged cries of a plaintive character, in all respects resembling those which the animal would utter from a distinct sense of pain. But the mere outward expression of pain is no proof of painful states of consciousness. Having already seen reason to exclude the mesencephale from the sphere of consciousness, we must regard these manifestations as merely the reflexly excited activity of an emotional expressive centre, which is likewise capable of being acted on from the higher regions of true conscious feeling. The phenomena observed in animals deprived of their hemispheres are in all respects analogous to those observed in human beings under the influence of chloroform. Chloroform first annihilates the excitability of the hemispheres, a condition coinciding with the abolition of consciousness, but the mesencephalic centres retain their excitability long after this point has been reached. Hence, impressions on nerves which, in normal conditions, would excite groans or cries, and also painful sensation, under this degree of anæsthesia, elicit merely the groans and cries. These, however, are no more indicative of conscious suffering than, as Dr. Crichton Browne has expressed it, are the notes produced by striking the keys of a pianoforte indicative of pleasure or pain on the part of the instrument. In other words, the æsthesis passes directly into kinesis, just as the depression of the key of the pianoforte passes into the vibration of the string.

Besides cries, bodily movements and attitudes characteristic of emotion may likewise be experimentally excited in animals deprived of their hemispheres. For this purpose it is necessary to choose an animal normally characterised by high emotional excitability. The following quotation from Vulpian's lectures (*op. cit.* p. 548) illustrates these facts:—'The rat is an animal admirably adapted for experiments of this kind. It is very timid, very impressionable; it bounds away at the slightest touch; the slightest sound causes it to start. A whistle or a *souffle brusque* like the angry spit of a cat, excites in it vivid emotion. Before you is a rat, from which I have removed the cerebral hemispheres. You see it remains perfectly quiet. I now whistle with the lips, and you see the animal has made a sudden start. Each time I repeat the same sound you behold the same effect. Those of you who have studied the expression of emotion in the rat, will recognise the complete identity of these with the ordinary emotional manifestations of this animal.'

These, and other experiments, which will be described in the following chapter, serve to show that emotional expression may be elicited in animals deprived of consciousness by removal of their cerebral hemispheres.

Thus far attention has been directed mainly to the general nature and character of the reactions of the mesencephalic and cerebellar centres, and the methods by which these reactions are stimulated. In the following chapter an attempt will be made to explain the mechanism of the centres individually concerned in these forms of functional activity.

CHAPTER V.

FUNCTIONS OF THE OPTIC LOBES OR CORPORA QUADRIGEMINA.

§ 29. The optic lobes of frogs (fig. 11, B), fishes (fig. 12, B), and birds (fig. 13, B), are structurally homologous with the corpora quadrigemina of mammals (fig. 5, 4, 5).

The superficial origin of the optic tracts from the optic lobes in frogs, fishes and birds, and from the anterior tubercles of the corpora quadrigemina in the lower orders of mammals, and the similar, though less apparent, connection of the optic tracts in the monkey and man with the corpora quadrigemina, through the medium of the corpora geniculata and their brachia or arms, would almost, without experimental proof, indicate that these ganglia have an important relation to vision. But it would by no means follow that these ganglia are the centres of vision, even though it should be found that destruction of them produces blindness. Destruction of the optic lobes would naturally break the continuity of the optic tracts, and so cut off the eyes from the perceptive centres. That these ganglia are not the centres of consciousness of visual impressions, or *sense* of sight, has already been indicated in a former chapter (§ 21), and experimental demonstration of this fact will be furnished subsequently (§ 65). This is further borne out by the anatomical investigations of Gratiolet and Meynert, which have led them to the conclusion that the optic tracts likewise enter into relations with the optic thalami, and with radiating fibres which proceed to the lateral and posterior regions of the cerebral hemispheres.

The facts of anatomy and those of physiological experiment mutually support the view that the corpora quadrigemina, though not the centres of conscious vision, are centres of co-ordination of retinal impressions with special motor reactions.

Flourens first experimentally demonstrated that the optic lobes were the centres of co-ordination between retinal impressions and movements of the iris. When the optic lobes on both sides were destroyed, vision was completely abolished, and the pupils ceased to contract when light was thrown on the retina. This is a proof that in the optic lobes there is an organic connection between the optic, and the oculo-motor nerve which supplies the circular or constringent muscle of the iris. This connection has an anatomical basis in the fact that the central nucleus of the oculo-motor, or third nerve, is situated in the corpora quadrigemina beneath the aqueduct of Sylvius, or canal which, as it were, tunnels these ganglia.

When one optic lobe is destroyed, blindness of the opposite eye is the result. As regards the action of the pupils, it is observed that bilateral contraction is capable of being induced through the one optic nerve. The action of the pupil is, however, more marked in the eye, the retina of which is directly stimulated by light.

This is an illustration of an important law, of which we have seen other examples in the spinal centres, and which, as Dr. Broadbent has shown, serves to explain many facts of cerebral paralysis, *viz.*, that movements which are normally associated together are bilaterally co-ordinated in each centre. The pupils are usually associated in action, and hence, owing to the bilateral co-ordination in each lobe, the destruction of one optic tract does not induce complete paralysis of the opposite pupil. The blindness of the opposite eye, which results from destruction of one side of the corpora quadrigemina, or one optic lobe, is readily accounted for by the decussation of the optic tracts in the optic chiasma or commissure. In fishes, the decussation is apparent without further dissection, for the one nerve merely passes below the other. In frogs, birds and the lower mammalia, the tracts decussate through each other; but anatomically and physiologically, it has been demonstrated that the decussation is a complete one. When one optic lobe is destroyed in a frog or bird, blindness occurs only in the opposite eye, and its optic tract and retina undergo degeneration. When one eye is removed, atrophy of the optic tract and opposite lobe results. When the anterior tubercle of the corpora quadrigemina on one side is destroyed in the rabbit, blindness occurs only in the opposite eye, and degeneration of the optic nerve of that eye follows (Mandelstamm). So, if one eye is destroyed, atrophy of the opposite tubercle ensues.

In the case of man it is usually taught that there is not a complete decussation of the optic tracts in the chiasma, but that each nerve supplies corresponding parts of both retinæ, *e.g.*, the right optic tract supplying the outer half of the right eye, and the inner half of the left eye, and *vice versâ* in the case of the left. Further, that in the anterior angle of the chiasma fibres pass directly from one retina to the other, and in the posterior angle fibres connect both centres together.

This disposition of the optic nerves has been made the groundwork of an explanation of the fact of single vision with two eyes. This theory, however, though apparently affording a simple explanation of the fact, has recently been disputed. Biesiadecki, Mandelstamm and Michel, claim to have demonstrated by histological examination, that a complete decussation of the optic tracts takes place in the chiasma in man, as well as in other animals. Mandelstamm ('Centralblatt für die Med. Wissensch.,' 1873, and von Gräfe's 'Archiv f. Ophthalmologie,' 1874) has further shown how cases of hemiopia from injury or disease of the optic tracts and commissure, may be explained without having recourse to the usually accepted doctrine. The clinical researches of Charcot, however, to be subsequently referred to (p. 168, fig. 45), tend rather to confirm the usually accepted view of incomplete decussation in man.

It is obvious, however, even on anatomical grounds, apart from physiological experiment, that this co-ordination of retinal impressions with irido-motor action in the corpora quadrigemina is far from exhausting the functions performed by these ganglia.

The corpora quadrigemina, or optic lobes, stand in no constant relation to the development of the eyes. These ganglia attain a considerable development in animals in which the eyes and optic tracts are rudimentary, or almost wanting. Among animals of this kind Longet enumerates various genera of *Moles* and *Shrews* in the class of mammalia; the *Proteus* and *Cecilia* in the class amphibia; and the *Apterichthys cæcus*, and

Myxine or *Hag* among fishes. In man, also, the corpora quadrigemina are relatively of less size than in the lower vertebrates.

§ 30. Serres ('Anatomie Comparée du Système Nerveux,' 1827) first intimated that destructive lesions of the corpora quadrigemina, besides causing loss of sight, caused disorders of equilibrium, and locomotor inco-ordination. These results were explained away by Longet and others as in reality depending on injury to the subjacent cerebral peduncles. More recently Cayrade ('Sur la Localisation des Mouvements Réflexes,' 'Journ. de l'Anat. et de la Physiologie,' 1868) showed that frogs from which he had removed the optic lobes, while retaining the 'coordination des mouvements partiels en mouvements généraux,' had completely lost 'l'harmonie et l'équilibration des mouvements d'ensemble,' such as those of leaping, swimming, etc. Serres' opinion receives support from these experiments. Similar experiments performed by Goltz have led him to conclude that the optic lobes in frogs are specially concerned in the function of equilibration.

Goltz found that frogs deprived both of cerebral hemispheres and optic lobes could still be made to spring away on irritation, but the movements were 'plump und unbeholfen.' Turned over on their back they managed to recover the usual position, but the feet were placed irregularly, and the body was supported more by the abdominal surface than by the limbs. The faculty of equilibration, however, as determined by the balancing experiment before alluded to, was completely lost; for a frog so mutilated would fall like a sack of flour when the basis of support was tilted.

It might be supposed that the loss of balance in this case is the result of the blindness caused by destruction of the optic lobes; but that this is not so is shown by the fact that a frog deprived of its cerebral hemispheres, and also of its eyes, is still able to maintain its equilibrium as before. If the optic lobes alone are destroyed, equilibration becomes impossible, even though all the other encephalic centres are retained.

These experiments seem to show that the optic lobes in frogs form an essential part of the central mechanism by which the muscular apparatus concerned in the maintenance of equilibrium is co-ordinated.

In a series of similar experiments which I made on fishes, I found that superficial injury to the optic lobes produced a manifest disharmony of movement, the animal swimming on one side or the other, or on its back, or rolling round on its antero-posterior axis, but never able to swim in the ordinary position. Entire removal of the optic lobes caused complete annihilation both of the powers of equilibration and locomotion. These phenomena were equally observed in fishes with or without their cerebral hemispheres. The presence or absence of hemispheres does not affect the general result. The only movement observable after complete removal of the optic lobes was a flap of the tail on cutaneous stimulation, but no further attempts at co-ordinated progression.

Lesion of the optic lobes in pigeons also causes disorders of locomotion and equilibration, in addition to loss of sight. ('Experiments on the Brain of Pigeons,' McKendrick, Trans. Roy. Soc. Edin. 1873.)

I have also found that in rabbits, disorganisation of the corpora quadrigemina causes blindness, with dilatation and immobility of the pupils, and also very marked disturbances of equilibrium and locomotion. While still capable of making co-ordinated movements of all four limbs on reflex stimulation, or when held up by the tail, they could neither stand nor walk, but rolled over from side to side. Equilibration and locomotion were completely annihilated in a rabbit in which I removed the whole brain by a section just anterior to the superior peduncles of the cerebellum. Reflex movements of the limbs were readily excited by cutaneous stimulation, but all efforts on the part of the animal to raise itself or move away from the irritant were utterly ineffectual. The animal was allowed to survive for twenty-four hours, but the phenomena remained unchanged; thereby showing that they were not the mere result of shock consequent on the operation, circulation and respiration going on quite regularly.

Lesion of the corpora quadrigemina in a monkey, caused symptoms in many respects similar to these.

With the view of breaking up these ganglia in the monkey, I passed a wire cautery in a horizontal direction through the anterior extremity of the left inferior occipital fissure (fig. 26, o_2), so as to traverse the nates, or anterior tubercles of the corpora quadrigemina. The result of this procedure, as proved by *post-mortem* examination fifteen hours afterwards (the animal being killed with chloroform) was that the nates were ploughed up and disorganised by the cautery. There was some effusion, and slight softening of the posterior aspect of both optic thalami, but the posterior commissure was not destroyed, and the corpora geniculata, testes, crura cerebri and optic tracts were uninjured. The posterior lobe of the left hemisphere was perforated and softened in the track of the cautery, and the wire had passed across the ganglia and sunk a line or two into the corresponding point in the internal aspect of the right hemisphere. (It will be seen subsequently (§ 71), that the lesions of the hemispheres here existing are not concerned in the causation of the phenomena which were observed in this case.) If there was any difference, the left tubercle was more extensively injured than the right.

The result of this lesion was that the animal was rendered completely blind, a fact which, among other tests, was ascertained some twelve hours after the operation, by its inability to discern the position of some milk which it was eager to reach, and which it drank greedily when the dish was held to its lips. The pupils were dilated and inactive, the left somewhat more than the right. For some hours the animal kept its eyes closed, and only opened them partially when roused, but there was no real ptosis, and before death the eyes could be freely opened. With the exception of sight the other senses were retained. Voluntary movements of the limbs were still made, and the animal could grasp firmly as before both with hands and feet.

The chief symptoms visible were in respect to equilibration and locomotion. The animal sat in a crouching attitude, with head bent down, resting itself on hands and feet, which were planted in strange and unnatural positions. In this attitude it sat very unsteadily, swaying backwards and forwards. When it attempted to move it would turn round, generally from left to right, and frequently tended to fall back, which it counteracted by sudden jerks forward, and forcible slaps on the floor with its tail.

These various experiments show that marked disturbances of equilibrium and locomotor co-ordination result from destructive lesions of the corpora quadrigemina or optic lobes.

§ 31. It was stated that animals deprived of all encephalic centres above the optic lobes were still capable of emotional expression, particularly as regards the utterance of cries or sounds normally indicative either of pleasure or pain. This was especially seen in Goltz's croaking experiment on frogs. The gentle stroking of the back of the frog deprived of its cerebral hemispheres uniformly excites croaking. Goltz found that the croaking entirely ceased when the optic lobes were destroyed. Hence he concludes that the optic lobes form the central mechanism of this responsive action. In rabbits, as described by Vulpian, plaintive cries, frequently repeated, can be elicited by severe stimulation of cutaneous nerves, such as of the tail, feet, etc. This I have confirmed. Cries, however, may still be uttered by rabbits in which the corpora quadrigemina have been destroyed. Vulpian draws a distinction between the cry which is induced by reflex excitation of the respiratory centre, which is merely a modified expiration, and the peculiar cry which is uttered when the corpora quadrigemina and pons Varolii are retained.

I have made several experiments, with the view of determining whether the corpora quadrigemina, as distinct from the pons, were specially concerned in this result. After disorganisation of the corpora quadrigemina, chiefly of the anterior tubercles, I found that cutaneous stimulation still excited cries of the same nature as before. On entire removal of the corpora quadrigemina by a section passing transversely through the posterior margin of the testes, though for two or three hours after the operation no cry could be elicited by cutaneous stimulation sufficient to excite active reflex movements of the limbs, yet afterwards cries were induced when the stimulation was made more intense. I was unable to distinguish clearly between the cries in this case, and those uttered by a rabbit in which the corpora quadrigemina were uninjured; but it seemed to me that they were not repeated in the same peculiar manner as before.

The more prominent effects, therefore, of destructive lesions of the optic lobes or corpora quadrigemina in the various animals experimented on seem to be blindness; paralysis of irido-motor and some oculo-motor re-actions; disorders of equilibrium and locomotion; and in frogs, and apparently in other animals, annihilation of certain forms of emotional expression.

§ 32. We may next inquire, whether any light can be thrown on these phenomena by the method of irritation or excitation of these ganglia.

The optic lobes or corpora quadrigemina, unlike the cerebral hemispheres, are susceptible of irritation by various kinds of stimuli, mechanical, chemical or electrical.

Mechanical irritation was found by Flourens to be without effect on centres higher than the corpora quadrigemina. The superficial layers, according to him, are not susceptible to mechanical irritation, but 'piqûre' of the deeper layers caused convulsive movements and contraction of the pupils. The convulsive action he attributed rather to irritation of the underlying cruri cerebri than to irritation of the proper ganglionic centres. The contraction of the pupils would be accounted for by irritation of the oculo-motor nucleus which lies under the aqueduct of Sylvius.

My own experiments on rabbits, however, show that when these centres are not exhausted by hæmorrhage or shock, or paralysed by narcotics, mechanical irritation of the anterior tubercles by puncture with a needle causes distinct signs of irritation. A slight superficial puncture causes the animal to start suddenly and bound away, shaking its head as if in a state of sudden excitement or alarm. This speedily subsides, and the animal exhibits no further symptoms, nor can the injury to the corpora quadrigemina be distinctly traced, so slight is the injury which is sufficient to excite these manifestations.

The optic lobes would also appear to be susceptible to chemical irritation, from the experiments of Setschenow before alluded to (p. 18).

The corpora quadrigemina are extremely sensitive to electrical irritation. The phenomena vary according to the position of the electrodes on the nates or testes.

On irritation of the surface of the nates or anterior tubercles in monkeys, I have observed the following results :—

Irritation of one side causes the opposite pupil to become widely dilated, followed almost immediately by dilatation of the pupil on the same side. The eyes are widely opened and the eyebrows elevated. The eyeballs are directed upwards, and to the opposite side. If the left tubercle is irritated the eyes are directed to the right, and up. The head is moved in the direction of the eyes. The ears are strongly retracted. With continuance of the irritation the tail becomes elevated, the legs extended, and the jaws firmly clenched, with the angles of the mouth retracted to their utmost. The arms are approximated to the sides, and drawn back flexed at the elbows. Ultimately, when the stimulation is kept up, a state of complete opisthotonus is produced. Irritation of the testes or posterior tubercles produces the same effects, but in addition, cries are excited varying in character from a short bark, caused by the slightest contact of the electrodes, to all varieties of vocalisation, when the stimulation is continued. The motor effects are shown, first on the opposite side of the body, but ultimately both sides become affected by the unilateral irritation.

In dogs and cats the results of irritation are in all respects similar. The same dilatation of the pupils, first of the opposite eye, the same direction of the head and eyes, the retraction of the ears, the clenching of the teeth, and retraction of the angles of the mouth, and ultimately general opisthotonus result from irritation of the nates. Irritation of the testes causes, besides these effects, every variety of vocalisation. The same effects as regards the nates and testes respectively I observed in the case of a wild jackal subjected to experimentation.

As regards rabbits, the effects are almost exactly the same. The pupils are dilated, the eyes opened, the eyes directed up, and to the opposite side, the ears retracted, the jaws clenched, and ultimately opisthotonus occurs. Irritation of the testes besides these effects causes the animal to utter cries.

The utterance of cries of various kinds is so readily excited by irritation of the testes, that I took it as an indication, in experimenting in this neighbourhood, that the electrodes were in contact with, or that the current was conducted to the testes, if the animal suddenly barked or uttered a cry.

Experiments on pigeons demonstrate a similar relation between irritation of the optic lobes and muscular movements of the body and limbs. Irritation of the optic lobe on one side causes the opposite pupil to become intensely dilated. The head is thrown back, and to the opposite side; the opposite wing raised and extended or flapped, and the feet, especially the opposite one, drawn up to the abdomen or occasionally extended. Stronger irritation causes both wings to be spread out and flapped. In frogs, irritation of the one optic lobe caused the head to be thrown back, and to the opposite side, and the legs, especially the opposite, to be extended suddenly. Simultaneous irritation of both lobes caused the head to be thrown back, the legs extended, and the arms to be approximated to the side of the body and rigidly clasped. The pupils were not perceptibly affected by slight stimulation, but on prolonged irritation, causing general opisthotonus, the pupils became widely dilated. Frequently a sort of croak was likewise elicited.

In fishes, irritation of one optic lobe caused the tail to be struck forcibly and bent to the same side, while the dorsal and anal fins were spread out and directed in the same manner as the tail; the pectoral fins being spread out horizontally. I have observed no action of the pupils, but usually on irritation, the eye on the same side was jerked forwards. In the case of fishes it is to be noted that the action is direct, *i.e.*, on the same side as irritation, and not crossed as usual.

It is far from easy to explain the exact signification of these results of experiment on the corpora quadrigemina, and to show the mutual relations of the complementary methods of destruction and excitation of these ganglia. It is, however, sufficiently evident that they perform more extensive functions than the mere co-ordination between retinal impressions and irido-motor action. The destruction of the corpora quadrigemina annihilates the manifestation of those functions which still remain practically unimpaired by removal of the cerebral hemispheres, *viz.*, equilibration, locomotion, and in some measure, emotional expression. We have, therefore, reason to believe that the corpora quadrigemina form an essential part of the central mechanism by which these are rendered possible. And there is an evident relation between the development of these ganglia and the degree of independence with which some of these functions are manifested after removal of the hemispheres. In fishes, frogs, birds and rodents, the corpora quadrigemina, as compared with the cerebral hemispheres, are relatively large, and in these animals particularly we find that removal of the hemispheres has less effect on equilibration and co-ordinated locomotion than in animals with more highly-developed hemispheres. The apparent retention of the power of forward progression in frogs after removal of the optic lobes, seems to me more of the character of mere change in position caused by sudden reflex movements of the limbs consequent on powerful reflex stimulation. For in several experiments which I have made I have found that when the optic lobes have been thoroughly removed from frogs, the animals cease to make true co-ordinated attempts at progression, and are unable to maintain their normal attitude.

I make no attempt to differentiate between the optic ganglia, as such, and the underlying tracts, for I do not think it possible to determine experimentally what are the functions of the mesencephalic ganglia and cerebellum, apart from their connections and relations to the crura and pons.

Though the effects of irritation of the optic lobes have an important clinical and diagnostic bearing, it is difficult to determine their exact relation to the mechanism of central co-ordination of the bodily movements concerned in equilibration and locomotion. Very complex movements of the head, trunk, limbs and facial muscles result from electrical irritation of the surface of these ganglia. The explanation of these phenomena is a subject on which differences of opinion may be entertained. It may be said that the effects are in reality due to conduction of the currents to underlying motor tracts or centres. This, however, is disproved by other facts. The strength of current sufficient to cause these movements is excessively weak, scarcely perceptible when applied to the tip of the tongue. Moreover, certain forms of irritation in which conduction can play no part likewise produce similar effects. This is especially seen in the vital irritation of inflammatory processes affecting these structures. The irritative effect of inflammation I had occasion to observe very carefully in a rabbit in which I had endeavoured to destroy the optic lobes by means of the cautery. After the operation no apparent results ensued, but twenty-four hours subsequently the animal began to suffer from attacks of trismus and opisthotonus, like those caused by electrical irritation of the corpora quadrigemina. It was found after death that the cautery had not touched the corpora quadrigemina, but had caused inflammatory adhesion of the posterior extremity of the hemisphere to the surface of the nates, which were in a state of active congestion, though not otherwise organically injured.

It seems to me that the phenomena of electrical irritation of the corpora quadrigemina are mainly of a reflex nature, and depend on the transference of irritation of sensory to motor centres and tracts. Flourens regarded the optic lobes as essentially similar in constitution to the spinal cord, a view which seems to be justified both by anatomical and physiological considerations. The optic tracts which originate from these ganglia may be regarded as homologous with the posterior roots of a spinal nerve. Though all the sensory relations of these ganglia are not quite clear, other special sensory tracts besides those of the eyes are brought into relation with motor centres in these ganglia. One of the roots of the fifth nerve is traced by Meynert to a layer of large cells which surround the central canal or aqueduct of Sylvius.

It is not possible by direct stimulation of a co-ordinating centre, to excite the activity of this centre in the way in which it is normally exercised. Though the medulla oblongata is the co-ordinating centre of the respiratory movements, it is impossible to excite the respiratory movements in the normal manner, by direct excitation of the medulla itself. Hence, even though, as the results of destruction of the corpora quadrigemina indicate, these ganglia should be the co-ordinating centres of the muscular actions concerned in station and locomotion, we should hardly expect that they could be excited otherwise than in a convulsive manner by irritation applied to the centres themselves.

The movements of the trunk and limbs which are produced by excitation of the corpora quadrigemina are such as are concerned in the maintenance of the normal attitude, and for purposes of progression. Irritation of the optic lobes in frogs excites movements of the head, trunk and limbs; in fishes, causes movements of the tail and fins; in birds, causes movements of the wings; and in mammals, complex movements of the trunk and extremities.

§ 33. Momentary irritation of the optic lobes, excites a reaction closely resembling the sudden backward start, which we see reflexly excited by the sudden approximation of an external object to the eyes. In this we have optical impressions co-ordinated with muscular action, the result of which is to withdraw the head and eyes from dangerous approach.

The trismus, and the contraction of the facial muscles, together with the general opisthotonus which result from powerful stimulation of the corpora quadrigemina in mammals, may be regarded as the physical manifestation of painful stimulation in general. The phenomena are of the same character as those which are induced by the irradiation of sensory irritation throughout the spinal centres, such as are observed in idiopathic or traumatic tetanus. The clenching of the teeth, with retraction of the angles of the mouth, which is such a common manifestation of painful stimulation of sensory nerves, may be accounted for by the structural connection of one of the sensory roots of the fifth nerve with the corpora quadrigemina.

The dilatation of the pupils, which is so readily induced by irritation of the corpora quadrigemina, is probably of the same nature, *viz.*, an indication or expression of sensory irritation. It is well known that sudden or painful stimulation of sensory nerves is associated with dilatation of the pupils. This reaction is produced through the medium of the sympathetic nerves, which act on the dilating fibres of the iris; for it has been found by Knoll (Eckhard's 'Beiträge,' 1869), that irritation of the corpora quadrigemina causes no dilatation when the cervical sympathetics have been divided. These results are in accordance with the theory of the co-ordination in the corpora quadrigemina of sensory impressions with the mechanism of emotional expression.

Another characteristic effect of irritation of the posterior tubercles of the corpora quadrigemina, is the excitation of cries, varying in character from the short and sharp cry, caused by momentary application of the electrodes, to loud and prolonged vocalisation, with the bodily movements above described, when the irritation is kept up for a longer period. The testes are not represented as distinct structures in the lower vertebrates, though their homologues may be found to exist, intimately bound up in the structure of the optic lobes. These results of irritation, taken along with the facts already described in the experiments of Goltz, in reference to the reflex excitation of croaking in frogs, and in the experiments of Vulpian, in reference to the plaintive cries elicited by painful stimulation of sensory nerves in rabbits deprived of their cerebral hemispheres, would seem to indicate that the corpora quadrigemina, and especially the posterior tubercles of these ganglia, are centres of responsive reaction between stimulation of sensory nerves and the respiratory and laryngeal mechanism concerned in vocalisation. It has been shown, however, that cries may still be elicited, even when the corpora quadrigemina are completely removed. These are capable of explanation by the constitution of the medulla oblongata and its relation to the respiratory mechanism, and they evidently differ in character from the emotional cries which are effected through the agency of the corpora quadrigemina.

The foregoing considerations on the relation between the phenomena of irritation and destruction of the corpora quadrigemina, though in many respects professedly only of a hypothetical nature, tend to support the view that these ganglia are the centres specially concerned in the reflex expression of feeling or emotion. This is rendered still more probable by the recently demonstrated influence which the corpora quadrigemina, or more properly, the deeper parts of the corpora quadrigemina, exert on the functions of circulation and respiration, modifications of which are one of the most frequent concomitants of states of feeling or emotion. Danilewsky (Pflüger's 'Archiv für Physiologie,' Band xi., 1875) has published the results of an investigation which in a great measure have anticipated those of a similar research, in which Dr. Lauder Brunton and myself had been for some time engaged, with reference to the influence of electrical irritation of the brain and its ganglia on the circulation and respiration. Danilewsky has found—and in this our experiments quite agree with each other—that electrical irritation of the interior of the corpora quadrigemina causes a great rise in the blood pressure with slowing of the heart and amplification of the pulse waves. The respiratory rhythm is also altered in a marked degree; irritation causing a deep inspiration, followed by prolonged and powerful expiratory efforts. Danilewsky finds that similar modifications of the circulation and respiration may also be caused by irritation of the nucleus lenticularis, or that part of the corpus striatum which is in more immediate relation to the expansion of the cerebral peduncle, and also to some extent by irritation of the grey matter of the hemisphere overlying this region. It is very doubtful, however, whether the effects in this case are in reality due to localised irritation; and it is of importance to note that removal of the hemispheres does not cause any appreciable alteration of the blood pressure or respiratory rhythm, and that the effects of irritation of the deep parts of the corpora quadrigemina are capable of being produced when the hemispheres are destroyed.

These changes in the circulation and respiration, caused by irritation of the interior of the corpora quadrigemina, are precisely of the same nature as those which are observed on sudden or powerful irritation of sensory nerves.

In addition to these facts, it has been stated by Valentin and Budge that irritation of the corpora quadrigemina has a direct influence on the viscera, causing contractions of the stomach, intestines and bladder. These effects, if well established, would be another proof of the relation of the corpora quadrigemina to the reflex manifestation of emotion, for it is well known that under certain forms of emotion contraction of the intestines and bladder may occur, as shown by the sudden expulsion of their contents. Monkeys, in particular, express terror in this manner.

CHAPTER VI.

FUNCTIONS OF THE CEREBELLUM.

§ 34. The functions of the cerebellum form one of the most obscure and disputed questions in cerebral physiology. Apart from merely speculative notions, we find that even the positive facts of disease have been appealed to in support of diametrically opposed conclusions. This may seem strange, but will hardly be wondered at when the causes of uncertainty as to the nature of the data furnished by disease are fully taken into consideration. It is not enough simply to tabulate so many cases of disease of the cerebellum, and to found conclusions as to the functions of this organ, or the relation between the morbid appearances and the symptoms manifested during life. The effects of disease must vary, according as the lesion excites or destroys the function of the organ in which it primarily shows itself; according as it is abrupt or of slow growth; and, perhaps of more importance than either of these conditions, according as the lesion is direct and limited to the cerebellum, or indirectly affects the functional activity of the other nervous centres and subjacent structures. These conditions have been too often ignored, and cases have been classified together between which there is little or no agreement, and often the utmost possible divergence.

Though the facts and conclusions of experimental physiology are not free from discrepancies, yet more reliable data have been furnished by this than by any other method of investigation into the functions of the cerebellum.

The researches of Flourens form the starting point of the first clearly defined notions respecting the functions of this organ, based on reliable inductive methods.

In the preceding chapters we have already considered the nature and character of the functions which are manifested by animals entirely deprived of their cerebral hemispheres.

We had arrived at the conclusion that these functional manifestations, however complex and adaptive, furnished no grounds for the supposition that they implied intelligence or volition. The cerebellum, therefore, would be excluded from the sphere of mind proper, meaning by that the domain of conscious activity, a conclusion which at the very outset opposes the localisation in the cerebellum of any truly mental function, whether in the region of sensation, emotion, volition or intellect. Experimental research clearly points to the cerebellum as forming an essential part of the central mechanism by which external impressions are immediately co-ordinated with certain responsive actions, and furnishes no evidence in support of the existence of any form of spontaneous or self-determined activity, characteristic of animals possessing their cerebral hemispheres. Animals retaining their cerebellum along with the mesencephalic ganglia only react to immediate sensory impressions, but otherwise remain in absolute inaction, manifesting neither feeling, desire, nor will, until death ensues, unless nutrition is artificially kept up.

It has been seen that the faculties of equilibration, of co-ordinated progression, and of instinctive emotional expression are independent of the activity of the cerebral hemispheres, being equally well manifested by animals deprived of their cerebral hemispheres as by those in the normal conditions. Lesions of the cerebellum cause very remarkable disturbances, both as regards equilibrium and locomotion, whether the hemispheres exist or not. Flourens thus describes the results of injury to the cerebellum in pigeons: 'I removed the cerebellum of a pigeon in successive slices. During the removal of the first layers there appeared only a weakness and want of harmony in its movements. On removal of the middle layers the animal exhibited a general agitation without true convulsions. It made brusque and irregular movements, and continued both to see and to hear. On removal of the last layers the animal entirely lost the power of standing, flying, leaping or walking, which had been gradually affected by the preceding mutilation. Placed on its back it was unable to rise. Instead of remaining quiet and immovable, like pigeons deprived of their hemispheres, it was in a continual state of restlessness and agitation, but could never make any determinate movement. It could see a threatened blow, and tried to escape, but without success. It made various ineffectual efforts to recover its station when laid on its back, but utterly failed to do so. Sensation, volition, and intelligence remained; the possibility of making *mouvements d'ensemble* persisted also, but the co-ordination of these movements into regular and determinate movements of progression was entirely lost' (*op. cit.* p. 37). Numerous similar experiments on pigeons gave results in all respects identical with these; lesions of the cerebellum in all cases causing loss of co-ordination, varying from the swaying and reeling of slight intoxication to utter disorder of movements, according to the extent of the injury inflicted. In no instance did there appear to be any interference with sensation or intelligence.

Flourens also demonstrated that essentially the same results followed lesions of the cerebellum in many other birds, as well as in numerous orders of mammals. In mammals, as in birds, superficial lesion caused disharmony of movements, a disharmony which increased in proportion to the extent of the lesion; while total destruction of the cerebellum entailed the entire loss of all power of progression.

Flourens concluded from these experiments that there exists in the cerebellum a 'propriété qui consiste à *coordonner* les mouvements *voulus* par certaines parties du système nerveux *excités* par d'autres.' The facts described by Flourens, and the explanation given by him of these facts, are things which ought to be kept separate, and not confounded together, as has so often been done by many who have written on the subject. If we take the experimental data alone, apart from the theory founded on them by Flourens, we find that they have in the main been confirmed by all subsequent experimenters on birds and mammals. That lesions of the cerebellum in these animals cause disorders of movement resembling those of intoxication in varying degree, may be regarded as a thoroughly well-established fact.

As regards the duration of these effects, however, much depends on the extent of the lesion. Flourens found that superficial lesions, or even deep incisions into the substance of the cerebellum, might be ultimately recovered from, the animal again regaining stability and perfect co-ordination of movements. Complete removal of the cerebellum in birds, however, caused permanent disorders of equilibrium.

But as to duration, the experiments of Dalton, Wagner and Weir-Mitchell are not quite in accordance with those of Flourens. Weir-Mitchell states that some pigeons, from which he had removed the greater portion of the cerebellum, and practically annihilated the functional activity of the whole organ, ultimately —after a lapse of months—recovered so far as to show only feebleness and incapacity for prolonged muscular exertion, but no real inco-ordination or unsteadiness of equilibrium. Whether these negative results are capable of explanation, in harmony with the undoubted fact that lesions of the cerebellum do cause marked disorders of equilibrium, is a question which will be discussed below. This apparent recovery is only proved experimentally in the case of pigeons which survive extensive mutilation of their encephalon. In regard to mammals we have no such experimental data, as it is impossible to keep them long alive after such severe operations as destruction of the cerebellum. In reference to this question the results of disease of the cerebellum in man require therefore to be specially considered.

But when we turn to the recorded cases of disease of the cerebellum in man, we find many facts which it is difficult to reconcile either with those of experiment on animals, or with Flourens' hypothesis. There are some cases on record in which disease of the cerebellum had existed during life without giving rise to any marked effect on co-ordination. Many of these, however, have been cases of superficial or comparatively slight lesion of the cerebellum, and such cases are not inconsistent with the statements of Flourens, that animals may ultimately recover from superficial lesions of this organ. The difference between the often slowly-progressive lesion of disease and the abrupt lesion of physiological experiment, would also help to explain away many difficulties in the way of a satisfactory explanation of other cases.

Andral ('Clinique Médicale') has collated ninety-three cases of disease of the cerebellum, and on analysis come to the conclusion that only one of them quite supports Flourens' theory, that the cerebellum is the organ of co-ordination of movements.

Andral, however, has classed together most heterogeneous cases, in which it is quite impossible to differentiate between the direct and indirect of the lesions, and even those who do not accept Flourens' interpretation of the functions of the cerebellum, regard Andral's data as exceedingly unsafe, and his conclusions far from being trustworthy. Even, however, when we eliminate all cases of disease of the cerebellum in which there has been manifest perturbation of the functions of the other encephalic centres necessarily caused by the very nature of the disease, there still remain numerous well-authenticated and carefully-recorded instances, which, though not opposed to Flourens' data, are not capable of being harmonised with his theory—stated without modification—that the cerebellum is the organ of the co-ordination of movements of locomotion. Many such cases might be quoted, but I select only one or two. One has been frequently referred to in discussions as to the functions of the cerebellum, *viz.*, that recorded by Combette (' Revue Med.' 1831). This observer gives the particulars of the symptoms observed in a young girl in whom there was complete absence of the cerebellum. This patient could stand and walk up to a short period before her death, and the only characteristic symptom noted was that '*se laissait souvent tomber.*'

Another case, reported by Bouillaud, and referred to by Longet and Vulpian, is that of Guérin, whose cerebellum was found after death to be almost completely destroyed by disease. This patient still retained the power of co-ordination of movements and could walk, only he was observed to reel and totter when he walked.

In reference to this case Vulpian remarks, ' Here we have a case in which the cerebellum was destroyed, and yet the patient could walk, though in an unsteady manner. But if this (Flourens') hypothesis were well founded, he ought not to have been able to stand or walk a step, for the combination of muscular contractions necessary for locomotion or maintaining the erect attitude, ought to have been altogether impossible' (Vulpian, *op. cit.*, p. 633).

Admitting, as I think we must do, the force of this criticism, the important fact still remains, which is quite in harmony with Flourens' experiments, that in man also, lesions of the cerebellum cause disturbances of stability and locomotion, manifested more particularly in a reeling and uncertain gait, described by Hughlings-Jackson as the 'walk of a man slightly drunk.'

As regards the lower vertebrates, *viz.*, frogs and fishes, which have also been subjected to experiments, there is some discrepancy among investigators as to the effects of removal of the cerebellum.

Vulpian and Philipeaux found that destruction of the cerebellum in fishes caused no disorders of locomotion, unless the deep connections of the cerebellum were injured, in which case the phenomena were analogous to those observed in the case of mammals. From my own experiments on fishes, I find that destruction of the cerebellum does not interfere with the movements of swimming or their regular co-ordination; but I have invariably found after this lesion that the animals swim either on one side or the other, or on their back, but never preserve the normal attitude and balance. In such cases I have satisfied myself that the lesions were confined to the cerebellum, and that the results were not due to injury to subjacent tracts.

As regards frogs, Vulpian and Philipeaux also state that removal of the cerebellum does not cause any perceptible disorders of locomotion.

It is more difficult to trace any marked effect to the destruction of the rudimentary cerebellum in these animals, and it certainly does not destroy the power of co-ordinated progression, for frogs in which only the optic lobes are allowed to remain, still maintain their normal attitude, and leap away on irritation. Goltz, however, has noted that, just as in the experiments of Flourens on other animals, the movements are of an uncertain and unsteady character. Goltz also attributes to the cerebellum some of the functions which the optic lobes chiefly govern, *viz.*, co-ordinated locomotion. He finds that if the cerebellum alone of the encephalic centres is left, frogs can still leap away on irritation. Whether we are to regard the functions of the cerebellum and optic lobes as more intimately bound up with each other in the case of the frog than in other animals, it would be difficult to say definitely, but it is extremely probable, if Goltz's facts are correct. Exact differentiation is, however, more difficult in the case of the frog than in other animals, and the co-ordination of *mouvements d'ensemble* in their spinal centres is so much greater, that forward progression alone may be merely spinal reflex reaction.

It is not easy to determine whether other animals really retain the faculty of locomotion when the cerebellum alone exists, but I have found in fishes that when the cerebrum and optic lobes were both removed, the power of locomotion was annihilated, cutaneous irritation causing only reflex movements of the tail or fins. A change of position thus resulted, but no true co-ordinated act of swimming was induced. These facts, and those of disease in man, tend to show that the cerebellum is not specially concerned in the co-ordination of locomotion, a function which we have seen reason to localise in the optic lobes.

It is shown by the foregoing experiments, with a remarkable degree of uniformity in all classes of animals, that mechanical lesions of the cerebellum induce, in the first instance, if not permanently, such disorders of equilibrium that station and locomotion become difficult and sometimes altogether impossible. It is not that the muscles are paralysed, or that co-ordinated movements of locomotion are rendered impossible, for the animal still retains the power of voluntary motion, and the co-ordinated combinations of muscular contractions concerned in locomotion may be willed or excited as before, but these are no longer co-ordinated with the position of the body in space, and hence the animal in its attempts at locomotion, reels, staggers or flounders about in the most helpless manner.

§ 35. Many explanations have been offered of the mechanism of these remarkable disturbances of equilibrium. Brown-Sequard justly remarks that we must in all cases carefully guard against the danger of confounding the effects of lesion of an organ as such with the effects which are apt to follow from mechanical disturbance or irritation of neighbouring or subjacent parts during the necessary operative procedure. Keeping this in view, Brown-Sequard comes to the conclusion that the disorders of movement consequent on mechanical lesions of the cerebellum are in reality caused by irritation of neighbouring structures. While it must be admitted that lesions of subjacent and neighbouring parts may cause disorders of movement (a fact which is quite in harmony with the experiments on the corpora quadrigemina and pons Varolii), the theory that lesions of the cerebellum only act indirectly in this way, is by no means in accordance with the positive facts of carefully-conducted experiments of other investigators, and by different methods. Vulpian finds that lesions of the cerebellum produce disorders of equilibrium when the operations are made with every possible precaution against disturbance of neighbouring parts, and my experiments are quite in accordance with those of Vulpian. Weir-Mitchell also finds that freezing the cerebellum by means of ether spray causes disturbances similar to those resulting from mechanical destruction, a method which entirely avoids any indirect lesion of neighbouring structures. Destruction of the cerebellum by chemical substances and by the cautery, also induce disorders of equilibrium, facts which tend to dispose of the theory advanced by Brown-Sequard.

But while both Vulpian and Weir-Mitchell find that lesions limited to the cerebellum are sufficient to cause disorders of equilibrium, I cannot think that they are warranted in ascribing the results only to irritative lesions of this organ. Vulpian thinks that the fact that the disorders of equilibrium are most pronounced when the lesions affect the deeper parts of the cerebellum, parts which are susceptible of mechanical irritation, tends to show that the disorders are principally, if not wholly, due to irritation of the cerebellar peduncles. Weir-Mitchell is of opinion that the congestion which follows on freezing of the surface of the cerebellum, acts as a vital irritant. But in this latter case we have evidently to deal with a paralytic or passive congestion, a condition which is not coincident with active irritation, if we are to judge of the effects of freezing on other tissues and organs. Experiments by other methods, and on other parts of the encephalon, enable us to determine with little difficulty, when we have to deal with irritative and when with destructive lesions.

The result of mechanical ablation of the cortex of the hemispheres, which, like the cortex of the cerebellum, is insensible to mechanical irritation, is not irritation, as will be demonstrated subsequently, but destruction of the functional activity of the part; and we have no more reason to regard mechanical lesions as the cause of irritation in the one case than in the other. But besides mechanical lesions, lesions caused by other methods, such as by chemical agents and by the cautery, cause loss of function of the part, and not irritation. And when, moreover, it is considered that the disorders of equilibrium continue long after the immediate operative procedure, and long after any traces of active irritation have subsided, we cannot, in face of these facts, ascribe the disorders only to irritative lesions of the cerebellum.

I shall endeavour to show that irritative lesions and destructive lesions are both capable of causing disorders of equilibrium, but that the effects are quite opposed to each other.

Without, however, for the present, attempting to differentiate between the results of irritation and those of annihilation of function, we may regard it as a sufficiently well-established fact, that lesions of the cerebellum, as such, are capable of inducing disorders of equilibrium apart from indirect injury to neighbouring structures.

§ 36. Thus far we have only considered the general fact that lesions of the cerebellum cause disturbances of equilibrium, without attempting to determine whether the equilibrium is overthrown in one direction more than in another, according to the situation of the lesion. This, however, is deserving of careful consideration, as serving to throw considerable light on the mechanism of equilibration, and the real cause of the disorders which follow injury to the cerebellum.

Very great difficulties are encountered in the experimental determination of this question, owing to the position of the cerebellum, and the dangers of injury to other important structures inducing complications by no means easy to analyse, or refer to their exact cause. Hence, a fertile source of discrepancy among the results obtained by different investigators.

When the cerebellum is divided exactly in the median line in an antero-posterior direction, it is found that the disturbances of equilibrium, if any, are of no marked importance, and there is none of the tendency to reeling or rotation which characterises undefined lesion of the organ. It is also found that when lesions, which are as nearly as possible symmetrical on both sides, are made, that the disorders of equilibrium are also comparatively slight. When the lesions, however, are established unsymmetrically, or unilaterally, disorders of equilibrium are more manifest, and the equilibrium is overthrown in different directions, according to the position of the lesion.

When the anterior part of the middle lobe of the cerebellum (fig. 16, 3,) is injured the animal tends to fall forward, and in its attempts at locomotion usually stumbles or falls on its face (Flourens, Renzi). When the posterior part of the median lobe of the cerebellum (fig. 16, 2) is injured, the head is drawn backwards, and there is a continual tendency to fall backwards on attempts at locomotion. This fact I have determined by careful experiment on a monkey.

The occipital bone was removed over the torcular Herophili, and the tentorium divided carefully, so as to avoid laceration of the venous sinuses. With a red-hot wire the posterior part of the median lobe (*declive monticuli*, fig. 16, 2) was penetrated and broken up accurately in the median line, the lesion, as was ascertained *post mortem*, being found accurately circumscribed in the position indicated. Immediately on the operation, the animal's head was drawn back in tonic contraction. This lasted only a few seconds, and the animal on recovering from the narcotic stupor, on attempting to stand up fell supine. It could sit still holding on to some support, but on letting go tended constantly to fall, and frequently did fall on its back. When it tried to run it always tended to fall or stagger backwards. This backward tendency lasted during the day of the operation and nearly the whole of next day, when it was chloroformed to death in order that the lesion might be examined. As above stated, it was found that the grey matter of the posterior part of the middle lobe was disorganised. No other lesion existed in the cerebellum or elsewhere.

An important confirmation of these experiments is the clinical fact that a retraction of the head and tendency to fall backward, is a very common feature of disease of the middle lobe of the cerebellum. Though it is always exceedingly difficult to localise the extent of the influence of diseased conditions, the fact that retraction of the head so frequently accompanies disease of this part of the cerebellum, is of great significance in connection with these results of experimental physiology, and with other phenomena to be subsequently described.

With regard to the effect of lesions of the lateral lobes of the cerebellum, there is some difference of opinion as to the direction in which the disorders of equilibrium are manifested. It was found by Majendie that division of the middle peduncle of the cerebellum caused the animal to revolve on its own axis with incredible rapidity towards the side on which the peduncle was cut, *e.g.*, if the left were cut the animal turned over and over from right to left. Animals so operated on, when placed in their cage among straw, turned so incessantly as to coil themselves up in the straw, like a bottle packed for transit. This experiment has been repeated by other physiologists, and confirmed by Schiff, Vulpian, etc., though Longet and Lussana describe the rotation as occurring towards the sound side.

The evidence, however, is in favour of the fact that the most usual direction in which rotation takes place is towards the injured side. When the rotation is about to occur, there is usually observed a very remarkable torsion or spiral twisting of the head and trunk, which seems to carry the animal irresistibly round on its longitudinal axis. Thus, on division of the left peduncle the head twists backwards and to the right, the left side of the face looks downwards, the dorsal aspect of the spine tends to the left and downwards, so that the thorax and fore limbs are directed upwards into the air. The result of this is to cause the animal to roll round on its axis from right to left. This rotation is accompanied by a remarkable deviation of the eyes, first observed by Majendie. The eye on the side of lesion looks downwards and inwards, while the eye of the sound side looks upwards and backwards. This upward and backward direction of the right eye coincides with the torsion of the neck backward and to the right, which with the torsion of the spine above described, results in the rotation of the whole body towards the left.

This is, however, to be understood of an animal supported on four limbs, with the vertebral axis parallel to the ground, as in rabbits. The same animal, pivoted on its hind limbs, would then be seen to spin on a vertical axis, and viewed from the front, would seem to revolve from left to right. We should, therefore, expect that in man, in whom the body axis is vertical, the same lesion which causes a quadruped to roll round and round with a direction towards the left, would cause an apparent spinning round from left to right. If the individual were placed on the ground in the position of the quadruped, the same impulse which causes the rotation on a vertical axis from left to right, would cause the body to roll towards the left side. This apparent difference in cases which are in reality identical, when the conditions are properly considered, may serve to explain some of the discrepancies in the statements as to the direction in which the equilibrium becomes disturbed as the result of lesions of the middle cerebellar peduncle.

I have spoken of lesion of the middle peduncle as if it represented the same lesion as direct injury to the lateral lobe itself, and practically such is found to be the case. Here also there is some difference of opinion as to the direction in which the equilibrium is disturbed; but most commonly, according to the recent researches of Hitzig ('Untersuchungen ü. das Gehirn,' p. 268), with which mine coincide, the rotation is towards the side of injury, when extensive lesion is made in the left lateral lobe. The animals in Hitzig's experiments rolled over and over to the side of injury with as great force as in Majendie's experiments of section of the middle peduncle.

Much, however, depends on the extent and situation of the lesion in the lateral lobe. If the lesion affects the whole of the lobe there is a tendency to roll over towards the affected side, *i.e.*, to revolve on a vertical axis towards the sound side. If the lesion is limited, the disturbance of equilibrium may not be so severe as to cause rotation, and the animal may fall towards the opposite side. Thus, I exposed the left lateral lobe of the cerebellum in a monkey, and by means of the actual cautery destroyed the surface of the posterior superior lobule (fig. 16, 4), to the depth of a quarter of an inch; the lesion, as was ascertained by careful *post-mortem* examination, being localised exactly in this region. At first the disturbance of equilibrium was very great, the animal tending to fall back and to the right side, but this movement was sometimes so strong and combined with spinal rotation, as to cause the animal to roll over on its left side. On repeated examination of the animal for a period of twenty-four hours, I found that the tendency to fall backward and to the right continued when the animal attempted to move. This experiment, carefully performed, shows that with limited lesion of the left lateral lobe, at a certain point, the tendency is to fall over on the opposite side.

In connection with these disturbances of equilibrium, consequent on lesions of the cerebellum, it has been noted that temporary or permanent deviations of the optic axes occur, or some degree of nystagmus or oscillation of the eyeballs. The relation of these phenomena to the other motor disturbances will be considered, after the results obtained by electrical irritation of the cerebellum have been described.

§ 37. In a paper published by me in the 'West Riding Asylum Reports,' vol. iii. 1873, I described certain remarkable phenomena, specially relating to the occurrence of ocular movements, on irritating various parts of the cerebellum in rabbits by the same method of electrical irritation which I had employed in the investigation of the functions of the cerebral hemispheres. (For the details of method and criticisms see Chap. VII.) Since then I have performed numerous similar experiments on the cerebellum of other animals, and especially of monkeys. I had found experimentation on the cerebellum of rabbits surrounded by great difficulties. These have increased rather than diminished in my subsequent experiments, so that I have often despaired of being able to obtain any satisfactory results. I have attempted the exposure of the cerebellum in many animals, but the mortality has been great, and I have succeeded in comparatively few. Though more extended investigation is desirable, the experiments which I have made on cats, dogs and monkeys entirely corroborate my experiments on rabbits in reference to the influence of irritation of the cerebellum on the ocular movements. They further bring out the relation of these movements to the bodily adjustments of equilibrium with which, as I had indicated, they were associated.

Electrisation of the Cerebellum of Monkeys.

The cerebellum in the monkey is so overlapped by the cerebral hemispheres, that it is impossible to expose it completely in any one case for experimentation. The following results have been obtained from experiments, more or less successful, on twelve monkeys, though only partial explorations could be made in some of them. The parts most accessible are the vermiform process and the superior and posterior aspect of the lateral lobes, though occasionally other regions were reached, as will be seen from the description.

FIG. 16.—The Cerebellum of the Monkey seen from Above and Behind. 1. Pyramid of the median lobe. 2. Declive monticuli or posterior extremity of the superior vermiform process. 3. Monticulus cerebelli or anterior extremity of superior vermiform process. 4. Postero-superior (semilunar) lobule of the lateral lobe of the cerebellum. (For further significance of numerals see text.)

FIG. 17.—The Cerebellum of the Monkey seen from the Left Side. 2. The declive monticuli. 3. The monticulus cerebelli. 5. The flocculus.

1. Pyramid of the Median Lobe (Pyramis Vermis) (fig. 16). —*Both eyes turn to the left or right in a horizontal plane*, according as the electrodes are applied to the left or right side of this part throughout its whole extent.

2. Upper Vermiform Process—posterior extremity (Declive Monticuli) (fig. 16, 2).—*Both eyes move straight downwards*, when the electrodes are applied directly on the middle of this prominence.

a. Declive Monticuli (left side) (fig. 16, *a*).—*Both eyes move downward and to the left.*

b. Declive Monticuli (right side) (fig. 16, *b*).—*Both eyes move downward and to the right.*

3. Upper Vermiform Process—anterior extremity (Monticulus cerebelli) (fig. 16, 3).

a. Middle line.—*Both eyes move directly upwards.*

b. Left side.—*Both eyes move diagonally upwards and to the left (no rotation).*

c. Right side. *Both eyes move diagonally upwards and to the right (no rotation).*

4. Lateral Lobe—Semilunar lobule (fig. 16, 4).

Left side.—*Both eyes move upward and rotate to the left.*

Right side.—*Both eyes move upward and rotate to the right.*

These results were obtained by frequent experiments in this part, and with a remarkable degree of uniformity, there being apparently no further differentiation of special centres in the posterior aspect of the lateral lobe.

Flocculus (fig. 17, 5).

I have only on two occasions been able to place the electrodes successfully, and without complication, on this region. *Both eyes rotate on their antero-posterior axes.*

The vertical meridians remained parallel, the upper extremity moving sometimes with, and sometimes contrary to the hands of the clock, according as the electrodes were shifted to different parts of the floccular region, but the exact situation of the electrodes in each case could not be accurately made out.

§ 38. Besides these ocular movements, certain movements of the head and limbs were likewise produced.

In some of my experiments, in which the head was maintained in a fixed position, so that the eyes might be watched conveniently—a method which I had adopted in my experiments on rabbits—only movements of the eyes and limbs, if any, could be noted, but when the head was allowed free play, I found that the movements of the eyes coincided with movements of the head.

Thus, on irritation of the anterior part of the middle lobe (monticulus), when the eyes moved upward, the head was thrown back. Occasionally a tendency to extension of the legs was observed, and some spasmodic movements of the arms, the extent and character of which could not be satisfactorily defined.

It may be said that the backward extension of the head and limbs was in reality due to conduction of the current to the corpora quadrigemina, irritation of which causes this effect in a very marked manner; but that this is not so is proved by the fact that irritation, conducted or directly applied to the testes, invariably excites a sudden bark or howl. This I have occasionally observed, when on irritating the anterior part of the cerebellum, I had accidentally approached too near the testes. This sudden outcry is a good test of the localisation or not of the irritation on the cerebellum itself. Hence, in the absence of such manifestation it is to be concluded that the throwing back the head, and the upward movement of the eyeballs, is the distinct result of irritation of the anterior part of the middle lobe of the cerebellum itself, apart from conduction.

The downward movement of the eyes which results from irritation of the posterior part, or declivity, of the upper vermiform process, is associated with a forward or downward movement of the head. The upward and outward (to the left or right) movement of the eyes resulting from irritation of the posterior-superior lobes, is accompanied with a backward and upward movement of the head, to the right or left, according as the right or left side of the cerebellum is stimulated.

With these movements of the head and eyes there are generally associated some movements of the limbs on the same side of the body, *i.e.*, on the left side when the left half of the cerebellum is irritated; but their exact character or extent it is extremely difficult to define, owing to their sudden and spasmodic character.

Along with these effects the pupils were observed to become contracted, on irritating the cerebellum. The contraction of the pupil is specially marked on the eye of the same side, and I have observed the pupil on one side, *i.e.*, the side corresponding to the half of the cerebellum exposed, remain contracted after the irritation by the electric current had been suspended for some time.

I have never observed any vomiting or sign of excitement of the generative organs in any of the animals experimented on, though I have specially directed my attention to these points.

It is also to be noted, in reference to electrical irritation of the cerebellum, that occasionally stimulation is absolutely without effect at first, and that after the lapse of some time, the phenomena follow with great precision. I have not been able to satisfy myself with respect to these variations, as to whether they depend on degrees of anæsthesia, or state of shock or not. From whatever cause, the excitability of the cerebellum is subject to variations, which render the investigation troublesome, and, unless sufficient care is taken, may easily lead to apparently contradictory results. Frequently after the application of the electrodes, a condition of nystagmus comes on and lasts for some time, so that unless due time is allowed for the subsidence of this irritation, the results of applying the electrodes to another part become so confused with the effects of the preceding, that analysis is impossible. The results above described are those which I have obtained after careful repetition on different animals, and with due regard to those precautions which I have indicated as being necessary.

§ 39. *Electrisation of the Cerebellum of Rabbits.*

The following results have been already detailed in the 'West Riding Asylum Reports,' vol. iii. 1873.

The cerebellum of the rabbit is divided into a number of lobules, more distinctly differentiated from each other than in the case of the monkey and other higher animals. I do not attempt a homological nomenclature, but simply describe the results in reference to the position of the electrodes, as indicated in the accompanying figures (figs. 18 and 19).

Median Lobe.

Upper part (1).—*Both eyes move to the right in a horizontal plane.*

Middle part (2).⎫ *Both eyes move to the left in a hori-*
Lower part (3).⎭ *zontal plane.*

From these results it would appear that the various divisions of the middle lobe differ in action as regards the lateral movements of the eyes. There is, however, no differentiation in the corresponding part of the brain of the monkey, the movement to the right or left depending on whether the electrodes were applied to the right or left side. I have not again verified these results on the rabbit, and therefore it is not improbable that these differences may be partly, if not entirely, due to the position of the electrodes as regards the middle line, a point the importance of which has been more particularly brought out in subsequent experiments. The essential fact, however, is the plane of the ocular movements.

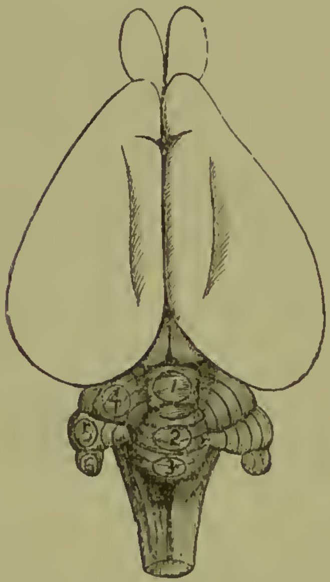


Fig. 18.—Upper Surface of Cerebrum and Cerebellum of Rabbit. The signification of the numerals is given in the text.

Lateral Lobe.—Left side.

Upper Lobule (4).—*Upwards with inward rotation of left eye; downwards with outward rotation of right eye.*

Middle Lobule (5).—*Upwards and rotation outwards of left eye; downwards and rotation inwards of right eye.*

Lower Lobule (6).—*Both eyes rotate to the right on their antero-posterior axes.*

Anterior Lower Lobule (7). Apparently the reverse rotation to that described under (6). (One observation only.)

(8.) Anterior part of the Cerebellum. (Position not exactly defined.) (One observation only.) *Both eyes moved upwards*, and then oscillated upwards and downwards.

Fig. 19.—Anterior aspect of the Cerebellum of the Rabbit. E is on the cut surface of the pons Varolii. The signification of the numerals is given in the text.

Besides these ocular movements, protrusion of the eyeballs and increased convexity of the cornea were noted, and also some dilatation of the nostrils.

Another recent experiment, without attempt at definite localisation, confirmed the fact of ocular movements, and also showed that movements of the limbs occurred on the same side as irritation. Twitching of the ears was also observed to occur during stimulation.

The general fact of movements of the eyes, limbs, nostrils and ears was also noted in some experiments on the cerebellum of rats. Localisation experiments were not, however, carried out on these animals.

I have also instituted experiments on the cerebellum of the cat and dog; several unsuccessfully, but in a few with a considerable degree of success as regards the extent of exploration and definiteness of the results.

§ 40. *Electrisation of the Cerebellum of Dogs.*

Median Lobe.

1. Pyramid (fig. 20, 1).

a. Left side.—*Both eyes move to the left.*

b. Right side.—*Both eyes move to the right.*

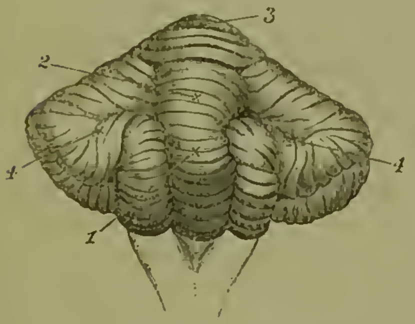


FIG. 20.—Cerebellum of the Dog, seen from behind and above. 1. Pyramid of the middle lobe. 2. Posterior extremity or declive of the superior vermiform process. 4. Postero-superior lobule of the lateral lobe of the cerebellum.

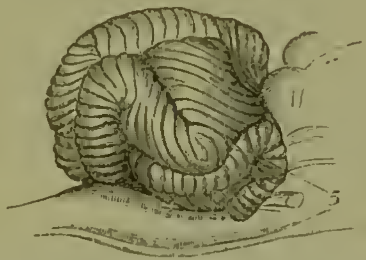


FIG. 21.—Right Side of the Cerebellum of Dog. 5. The flocculus.

Upper Vermiform Process.

2. Posterior Extremity (Declive) (fig. 20, 2).

a. Middle.—*Both eyes move downwards.*

b. Left side.—*Both eyes move downwards and to the left.*

c. Right side.—*Both eyes move downwards and to the right.*

3. *Lateral Lobe.*

4. Postero-superior Lobule (right) (fig. 20, 4). *Both eyes move upwards and to the right, rotating on their axes.*

This movement resulted from irritation applied to various points on this lobe.

5. Floccular Region (right) (fig. 21, 5).

Rotation of the eyeballs on their antero-posterior axes, sometimes to the right, sometimes to the left, according to the application of the electrodes on various points in this region, but the situation could not be determined with accuracy.

In the dog, also, I have observed movements of the limbs, nostrils and ears, during irritation of the cerebellum. Owing to the head being fixed, movements, if any, which might be caused were rendered impossible.

Experiments on the cerebellum of the cat led to essentially the same results from stimulation of corresponding regions, as will be seen by the following.

Electrisation of the Cerebellum of Cats.

Median Lobe.

1. Pyramid (here curved in the form of an S) (fig. 22, 1 *a*, 1 *b*).

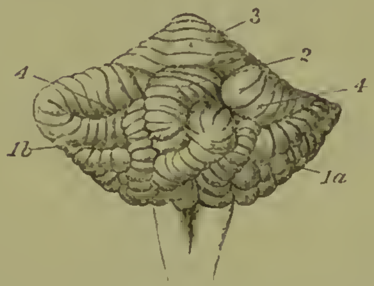


FIG. 22.—Cerebellum of the Cat, posterior-superior Surface. 1. S-curved pyramid of middle lobe. 2. Declive. 3. Anterior extremity of median lobe (monticulus). 4. Postero-superior lobule.

FIG. 23.—Left side of the Cerebellum of Cat. 5. Floccular region.

a. Right curve.—*Both eyes move to the right.*

b. Left curve.—*Both eyes move to the left.*

2. Upper Vermiform Process.

Posterior Extremity (declive) (fig. 22, 2).

a. Middle.—*Both eyes move downwards.*

b. Left side.—*Both eyes move downwards and to the left.*

c. Right side.—*Both eyes move downwards and to the right.*

Lateral Lobe (fig. 22, 4).

3. Postero-superior Lobule—various points.

Left.—*Both eyes move upward and to the left.*

Right.—*Both eyes move upward and to the right.*

Besides these movements of the eyeballs, it was observed that on irritation of the left side of the cerebellum the left pupil became contracted, and the left limbs were thrown into action. Movements of the head, if any, were not noted.

Both in the cat and dog the cerebellum is difficult to reach, and owing to the proximity of large venous sinuses, great and often fatal hæmorrhage results from attempts at complete exposure, hence, I have not succeeded in arriving at trustworthy conclusions in reference to the irritation of other regions.

These results, though incomplete, serve more particularly to indicate the homology of function between the cerebellum of the cat and dog and that of the monkey and rabbit, which were more fully and more frequently explored.

For the purpose of comparison some experiments were made on the cerebellum of pigeons and fishes (carp).

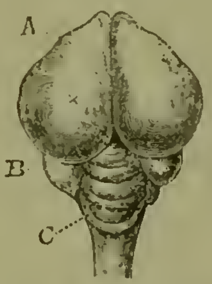


FIG. 24. Brain of Pigeon. C. The cerebellum.

§ 41. *Electrisation of the Cerebellum of Pigeons.*

Irritation of the cerebellum of pigeons causes no movements of the eyeballs, but, according as the electrodes are applied to the right or left side, the head is jerked backwards and to the same side, and frequently the wing of the same side is flapped and the leg drawn up.

Electrisation of the Cerebellum of Fishes (Carp).

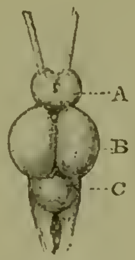


FIG. 25.—Brain of Carp. C. The cerebellum.

Irritation of the right side causes the eye on the same side to be jerked forwards, the tail to be bent to the right, and the fins spread out. Irritation of the left side causes exactly the same manifestations on the left side, while irritation on the middle of the cerebellum causes the eyes to be jerked forwards, the tail to be bent up towards the head, and the fins to be spread out—a state of opisthotonus.

§ 42. The experiments on the cerebellum of mammals throw considerable light on certain phenomena frequently observable in connection with disease or injury of the cerebellum, and explain, among other things, the occurrence of nystagmus, or of persistent ocular deviations, along with disturbances of equilibrium.

They receive a remarkable confirmation from, and confer an important significance on, the phenomena which are observed in man when a galvanic current is passed transversely through the skull in the cerebellar region. These phenomena were first described by Purkinje (‘Rust's Magazin,’ 1827), and more recently they have been very fully investigated by Hitzig (‘Untersuch. ü. das Gehirn,’ p. 198, *et seq.*) When a galvanic current of moderate intensity is passed through the head by placing the poles of the battery in the mastoid fossæ just behind the ears, the individual experiences a feeling of vertigo, in which the relation of his body to surrounding objects seems to be, or is, actually disturbed; or external objects seem to alter their relation to him. The direction in which the equilibrium is disturbed, or in which external objects seem to move, depends on the direction of the current through the head. When the positive pole, or anode, is placed in the right mastoid fossa, and the negative pole, or kathode, in the left, so that the current passes from right to left, at the moment when the circuit is closed, the head and body suddenly sink towards the anode, while external objects seem to whirl to the left. The direction in which external objects seem to move is compared by Purkinje to the motion of the tire of a wheel, standing parallel to the face, from right to left. When the eyes are closed the appearance of motion is transferred to the individual himself, who feels as if he were suddenly whirled from right to left, or as if the basis of support on the left side had been suddenly withdrawn. The direction is exactly reversed when the positive pole is placed on the left and the negative on the right side, or, while the electrodes maintain their former position, when the circuit is broken.

It has been found by Hitzig, that at the moment when the head moves towards the anode, the eyeballs are also moved in the same direction, and frequently are thrown into oscillations, or nystagmus. The deviations of the eyes are a combination of lateral and rotatory movements.

If we separate the objective from the subjective effects of the galvanic current directed through the head in this manner, we see, in the inclination of the head and eyes to the side of the anode, essentially the same phenomena as result from the direct application of the electrodes to the same side of the cerebellum; for, as is shown by the foregoing experiments, the predominant direction of the head and eyes is to the same side, with some degree of diagonal or rotatory motion. This gives us strong grounds for attributing the phenomena to irritation of the cerebellum on the side of the anode. This view is completely borne out by the results of Hitzig's experiments on the galvanic excitability of the cerebral hemispheres, in which he found that irritation proceeded almost exclusively from the anode. It is furthermore in accordance with the law of electrotonus that breaking the circuit reverses the condition of irritation, the kathode then becoming the point of stimulation. Hence it is, that at the interruption of the circuit the other half of the cerebellum becomes stimulated, and all the objective phenomena, viz., the inclination of the head and eyes, occur towards the opposite side.

But simultaneously with these objective effects, there occur certain modifications of consciousness which afford significant indications respecting the nature of cerebellar co-ordination. Modifications of consciousness must, however, be regarded as coincident only, and not an essential factor in cerebellar action. The fact that removal of the cerebral hemispheres annihilates consciousness and voluntary action, while it does not affect the function of equilibration, shows that the co-ordination of sensory impressions with special motor activity in the cerebellum, is an independent responsive mechanism. Hence it seems to me to be a radical error to account for the objective phenomena by modifications of consciousness such as the *feeling* of vertigo, or the *feeling* that support is withdrawn from one side of the body to the other. The subjective phenomena are only accompaniments of the objective, and depend, not on the cerebellum but on the cerebral hemispheres, just as reflex action may be accompanied by consciousness, though consciousness plays no part in the mechanism itself. Keeping these necessary distinctions in view, we shall be better able to interpret the relation between the objective and subjective phenomena consequent on irritation of the cerebellum. At the moment when the head and eyes incline to the side of the anode, external objects appear to be whirling to the opposite side. If, on the other hand, the eyes be kept shut, the individual himself feels as if he were being whirled in the same direction as the objects seemed to take when the eyes were kept open. The movement of external objects to the left, coincides, as Hitzig has correctly shown, with the ocular movements to the right when the anode is placed in the right mastoid fossa, and the current closed. Now this is precisely the direction in which objects seem to move when the eyes are suddenly deviated to the right. If the right eye is fixed on some object, and the inner side of the eyeball pressed on, the object appears to move to the left. In like manner, if the eyeball is pushed to the left, the object will appear to move to the right; and so it will seem to move up or down, according as the eyeball is pushed downwards or upwards respectively.

Further, if the body be whirled rapidly on a vertical axis in the direction from right to left, external objects will appear to revolve from left to right, an appearance which continues for some time after the rotation has stopped, owing to the persistence of retinal impressions. A feeling of giddiness or insecurity comes on if external objects seem to revolve, and the compensatory action necessary for maintaining the equilibrium is, in the case of rotation to the left, inclination of the head and body to the right side, and deviation of the eyes to the right, in order to keep the objects in view, and thus prevent their passing out of the field of vision. The direction of the eye to the right by voluntary effort, when the body has been whirled from right to left, is sufficient to stop the apparent movement of objects which continues after the rotation has ceased.

From these facts it appears that the effect of irritation of the right side of the cerebellum is the natural compensatory action which coincides with a feeling of being revolved from right to left, and this is shown very conclusively by the fact that when the eyes are shut the feeling of rotation to the left is the only sensation experienced, and that, too, even when the body is actually inclining to the right side.

The right side of the cerebellum, therefore, co-ordinates the muscular mechanism which prevents the displacement of equilibrium towards the opposite side, and this involves movements of the head, eyes and limbs on the right side. These are the actual results of the direct application of the electrical stimulus to the cerebellum itself. In like manner, the movements which result from irritation of the anterior part of the middle lobe of the cerebellum, viz., the backward movement of the head and extension of the trunk and limbs, together with the upward movement of the eyes, are to be regarded as the natural compensatory efforts to counteract a seeming rotation forward on a horizontal axis. We may suppose, therefore, that the subjective side of these objective phenomena is a feeling of being revolved like a wheel from behind forwards on a horizontal axis.

Similarly, the forward movements of the head and downward direction of the eyes resulting from irritation of the posterior part of the median lobe, are the compensatory or antagonistic actions to counteract a disturbance of the equilibrium in the opposite direction, *i.e.*, from before backwards. Hence we may suppose that irritation of this part coincides with the sensation of rotation like a wheel on a horizontal axis from before backwards.

The cerebellum would, therefore, seem to be a complex arrangement of individually differentiated centres, which in associated action regulate the various muscular adjustments necessary to maintain equilibrium of the body; each tendency to the displacement of the equilibrium round a horizontal, vertical or intermediate axis, acting as a stimulus to the special centre which calls into play the antagonistic or compensatory action.

Every form of active muscular exertion must tend to overthrow the balance, and we should therefore expect, on the above hypothesis, that the cerebellum would be developed in proportion to the variety and complexity of the muscular activity of which the animal was capable; a relation which is fully borne out by the facts of comparative anatomy (Owen). We should, further, expect to find that a lesion which annihilates the functional activity of any of the individual cerebellar centres, should manifest itself in a tendency to the overthrow of the balance in the direction naturally opposed by this centre. This also is in accordance with the facts of experiment. We have seen that stimulation of the anterior part of the middle lobe excites the muscular combinations which would counteract a tendency to fall forwards. Hence destruction of this part shows itself in a tendency to fall forwards. In this we see both the negative effect caused by the removal of the one centre, and the positive effect exerted by the unopposed and antagonistic centres.

In like manner stimulation of the posterior part of the middle lobe calls into play the muscular adjustments necessary to counteract a backward displacement of the equilibrium, and hence, as we have seen, destruction of this region manifests itself in a tendency to fall backwards.

The lateral lobes of the cerebellum contain centres for complex adjustments against lateral, combined with diagonal and rotatory displacements to the opposite side; and hence, as has been found by experiment, lesions of the lateral lobes exhibit themselves in disturbances of the equilibrium, either laterally, to the side opposite the lesion, or as the resultant of lateral and rotatory displacement in rolling over to the side of lesion. The effects of lesion of the lateral lobes may therefore vary, a fact which may account for some of the discrepancies among the results obtained by different experimenters.

§ 43. The mechanism of cerebellar co-ordination is essentially independent of consciousness or volition, and is an example of responsive or æsthetiko-kinetic action. But while we may theoretically in all animals, and practically in many, abolish consciousness and volition by removal of the cerebral hemispheres, and still leave the mechanism of equilibration intact, yet in the normal state cerebellar activity is associated with that of the hemispheres, and it is this association which serves to explain many of the facts which would seem to oppose the view which we have taken of the function of the cerebellum as a whole, and of its individual parts.

The displacement of the equilibrium in any direction not only calls into play by reflex action the compensatory motor adjustments, but also induces conscious or voluntary efforts of a similar antagonistic or compensatory nature. Thus a tendency to fall forwards, while reflexly calling into action the muscular combinations which pull the body backwards, may also excite consciousness and cause voluntary effort in the same direction. The same muscular adjustments which are capable of being effected by the cerebellum, are also under the control of the will, and may be carried out by the cerebral hemispheres independently of the cerebellum.

Hence it is that lesions of the cerebellum, while interfering with the mechanical adjustments against disturbance of the bodily equilibrium, do not cause paralysis of voluntary motion of the muscles which are concerned in these actions. This is an exceedingly important fact which, though disputed by some, seems to be established experimentally beyond all question. During the wildest reeling and tumbling of pigeons and other animals in which the cerebellum has been destroyed, there is no sign of muscular paralysis, and I have carefully investigated the condition of the muscular system in monkeys, in which lesion of the cerebellum had caused such disorders of equilibrium that locomotion was impossible, and have found that voluntary movements of the head, trunk and limbs were freely carried out in the recumbent position. The facts on which the statement has been founded that lesions of the cerebellum produce paralysis of motion on the opposite side of the body, are susceptible of quite a different interpretation. It has been observed that tumours, or apoplectic extravasations into one half of the cerebellum, frequently coincide with hemiplegia of the opposite side of the body. But in these cases, as Vulpian has rightly indicated, the hemiplegia is not the result of the cerebellar lesion as such, but of compression of the subjacent tracts of the pons and medulla. As these decussate in the medulla oblongata, the effect of compression by a tumour of the lateral lobe of the cerebellum is paralysis on the opposite side of the body.

Lesions of the cerebellum which do not exert a compressing influence on the subjacent tracts, do not cause hemiplegia on the opposite side. The lateral lobe co-ordinates muscular adjustments on the same side of the body, but as these are called into action by reflex stimulation, it is only this form of co-ordination which is suspended by lesions of the cerebellum, a condition, however, which is essentially distinct from paralysis of voluntary motion. The effect, whatever name it may be best designated by, is direct and not crossed.

In terming the effect of cerebellar lesion a paralysis of reflex adjustment, I do not thereby imply a paralysis of reflex action. This, which would result from spinal lesion, must necessarily coincide with paralysis of voluntary motion, as the path from the hemispheres would thereby be interrupted. What is implied is that the same combinations of muscular action which are co-ordinated in the cerebellum for the maintenance of the equilibrium, are capable of being called into voluntary action by the cerebral hemispheres. Hence, though lesions of the cerebellum destroy the self-adjusting co-ordination of muscular combinations necessary to maintain the equilibrium, they do not cause paralysis of voluntary motion in the same muscles. So, conversely, by removal of the cerebral hemispheres we cause paralysis of voluntary motion, but do not affect the independent mechanism of cerebellar co-ordination. When we make this necessary distinction we are enabled to understand how limited lesions of the cerebellum may produce only transient effects, and how even complete destruction of the cerebellum may ultimately be recovered from.

The disturbance of equilibrium is always most marked immediately after the infliction of injury to the cerebellum. This is to be accounted for by the sudden derangement of the self-adjusting mechanism on which the maintenance of the equilibrium mainly depends. As, however, the animal may supplement the loss of this mechanism by conscious effort, in process of time it acquires the power of voluntary adaptation, and thus is enabled to maintain its equilibrium, though perhaps with a less degree of security than before.

The more extensive the lesion, the greater the disturbance of the mechanism, and the greater the difficulty of effecting through conscious effort all the muscular adjustments necessary to maintain the balance. The disturbances of equilibrium are therefore of a more enduring character, and it is only by a long process of training that volitional acquisition can replace a mechanism essentially independent of consciousness. Even should this point be reached, the constant attention necessary to prevent displacement of the equilibrium would be a heavy strain on the animal's powers, and it would be quite in accordance with this condition, that prolonged or varied muscular effort should cause great apparent exhaustion. This is, in fact, what Weir-Mitchell observed in the case of some pigeons, which after many months had again recovered steadiness in their movements, notwithstanding extensive destruction of the cerebellum. In these he observed that great fatigue was induced by active muscular exertion, and on this he founded his theory that the cerebellum was a source of energy to the other nerve centres. By sparing higher centres the cerebellum may in one sense be regarded as a source of energy, but the real cause of the fatigue observed in the case of his pigeons is not the loss of any hypothetical reservoir of energy which is supposed to be continually streaming out, but a direct consequence of strained attention and conscious effort.

If it were possible to remove both cerebellum and cerebral hemispheres from a pigeon without causing speedy death, it might confidently be predicted that no recovery of the power of equilibration could ever take place.

A similar explanation is applicable to those cases of disease of the cerebellum which have been found to co-exist with little or no disturbance of equilibrium during life. A slowly progressive lesion would be the most favourable condition for the supplementation by conscious effort of a self-adaptative mechanism which is gradually undergoing degeneration. It is questionable, however, whether in man perfect substitution is possible; a want of precision and energy in movement, and a continual tendency to reel or fall being generally observable in cerebellar disease.

§ 44. In a former chapter (Chap. IV.) the maintenance of the bodily equilibrium was shown to be an example of adaptive, responsive, or æsthetiko-kinetic action, depending on the coordination in some central organ of certain afferent impressions with special motor adjustments. The afferent factors of this mechanism were shown to be mainly of three kinds, viz., tactile, visual, and labyrinthine impressions, and it was seen that marked disturbances of equilibrium resulted from perversion or interference with any part of this afferent system. The foregoing experiments on the cerebellum justify the conclusion that the cerebellum is the central organ of this co-ordination. This view is further confirmed by a comparison of the disturbances of equilibrium, consequent on lesions of the cerebellum, with those resulting from morbid affections of the afferent apparatus; as well as by a consideration of the anatomical relations of the cerebellum itself.

The afferent impressions conveyed to and calling forth the action of the cerebellar centres were regarded as physical in contradistinction to psychical modifications, and though under normal conditions these may be coincident with modifications of consciousness, consciousness is neither essential, nor is it a correlative of cerebellar action as such.

We should not expect, therefore, that lesions of the cerebellum would cause any affection or paralysis of either tactile, visual or auditory sensation properly so called, even though a direct connection of these nerves with the cerebellum should be anatomically demonstrated.

In reference to this point, however, there have been differences of opinion, and a separate consideration of each will be advisable.

The cerebellum was at one time regarded as the *sensorium commune*, or seat of common sensation. This opinion was founded chiefly on the continuity of the posterior columns of the spinal cord with the restiform tracts (3, fig. 3), or inferior peduncles of the cerebellum. This continuity has been denied by some, but the recent investigations of Meynert seem to establish the fact that the restiform bodies are continuations of the posterior columns in cross relation to each other, the restiform body on one side being in connection with the opposite posterior column. The posterior columns being regarded as the path of common or tactile sensation, the opinion that the cerebellum was the organ of tactile sensation seemed justified. But we have seen that the most recent investigations into the functions of the spinal cord do not support this view of the functions of the posterior columns, for tactile sensation is not abolished by section of these tracts. Brown-Sequard has also shown that section of the restiform bodies does not cause loss of tactile sensation. When we take these facts, in conjunction with the results of experimental physiology and the data of human pathology, we have overwhelming evidence against the view that lesions of the cerebellum cause loss of tactile sensation. Flourens, Vulpian, etc., have observed no indications of cutaneous anæsthesia in animals deprived of their cerebellum, and my own experiments on monkeys are in complete accordance with these results; cutaneous sensibility being retained intact after extensive cerebellar lesion. Nor do the facts of disease of the cerebellum in man afford any grounds for supposing that tactile sensibility is affected.

Lussana has put forward the theory that lesions of the cerebellum destroy the muscular sense, and to this he ascribes the disorders of equilibrium which ensue. This hypothesis is at variance with the clinical history of diseases of the cerebellum, and receives no support from physiological experimentation. Affections of the muscular sense never occur in man without other forms of tactile anæsthesia. It is extremely difficult to test the muscular sense in the lower animals usually selected for experiment, but I have observed monkeys, which owing to lesion of the cerebellum, were unable to maintain their equilibrium handle and grasp objects with as great precision and firmness as before—actions entirely inconsistent with loss either of tactile or muscular sensibility. Clinical observation of cases of disease of the cerebellum establishes the same. These facts, however, do not invalidate the view that it is through the restiform bodies that the cerebellum is brought into relation with certain forms of tactile impressions, which serve to excite the due co-ordination of the muscular adjustments requisite for equilibration.

§ 45. The auditory nerve is in direct connection with the cerebellum through the medium of the restiform bodies, as has been demonstrated by the researches of Lockhart-Clarke, and Meynert. Indeed Meynert is of opinion that the whole of the roots of the auditory nerve pass into the cerebellum in the first instance, and that therefore they can only have an indirect connection with the cerebral hemispheres, probably through the superior peduncles of the cerebellum, or the valve of Vieussens. This view is evidently untenable, for, as will be afterwards shown, there is a special region of the cerebrum, destruction of which abolishes the sense of hearing (§ 66); and the sense of hearing does not appear to be affected in animals deprived of their cerebellum. The facts of clinical medicine and pathology speak in the same way; for nothing is more rare than affections of hearing in connection with cerebellar disease, and then only when the lesion is of such a nature as to directly affect the auditory nerves. We have seen, however, the essential importance of impressions derived from the labyrinth in the mechanism of equilibration, and this connection of the auditory nerve with the cerebellum, is an anatomical confirmation of the view that the cerebellum is the central organ of equilibration.

There is, further, a remarkable similarity between the effects of lesion of the semicircular canals, and injury or removal of certain parts of the cerebellum. Flourens' experiments on the semicircular canals show that lesions of the superior vertical canals cause displacement of equilibrium forwards round a horizontal axis, an effect which corresponds with injury to the anterior part of the middle lobe of the cerebellum. Lesions of the posterior vertical canals cause displacement backwards round a horizontal axis, an effect which corresponds with injury to the posterior part of the median lobe. Lesions of the horizontal canals cause lateral or rotatory displacements round a vertical axis, an effect which corresponds with injury to the lateral lobes of the cerebellum.

The experiments of Mach and Crum-Brown have further shown that rotation backwards round a horizontal axis coincides with increased tension in the ampullæ of the superior vertical canals, and diminished tension in the ampullæ of the inferior vertical canals. Rotation forward round a horizontal axis causes a reversal of these conditions, and coincides with increased tension in the posterior vertical, and diminished tension in the ampullæ of the superior vertical canals. Lateral rotation round a vertical axis causes increased tension in the ampulla of the horizontal canal on the side from which rotation takes place, *i.e.*, in the left ampulla, if the rotation is from left to right, and corresponding diminution of tension in the ampulla of the canal on the side towards which rotation takes place.

Now we may suppose that in the normal condition these symmetrical plus and minus variations in opposed ampullæ are capable of balancing each other, so that the diminished tension which coincides with a lateral displacement of the equilibrium to the right, acts as a stimulus to the compensatory or antagonistic centre on the left. In like manner, the diminished tension in the posterior vertical ampullæ which would result from backward displacement of equilibrium, may be supposed to act as the stimulus to the posterior part of the middle lobe; and the diminished tension in the superior vertical ampullæ, resulting from forward displacement of the equilibrium, would in the same way act as the stimulus to the anterior part of the middle lobe, and call into play the extensors of the head and trunk.

Should, however, the one limb of this mechanism act in excess of the other, either as the result of abnormal irritation of the ampulla or of the opposite cerebellar centre; or as the result of removal of the antagonistic mechanism, either by lesion of the afferent apparatus or injury to the cerebellum, the balance will be overthrown in the direction of the unopposed or predominant force. This, as I have elsewhere endeavoured to show ('Labyrinthine Vertigo': 'West Riding Asylum Reports,' vol. v.) furnishes the explanation of the curious phenomena of Ménière's disease. In this there seems to be abnormal irritation of the ampullæ of the semicircular canals, and consequently there is a tendency to, or actual, overthrow of the equilibrium in the direction which corresponds with this condition, *i.e.*, to the right, when the irritation is in the left horizontal ampulla; backwards, when the irritation affects the superior vertical; and forwards, when the irritation is in the posterior vertical ampulla. There is still an effort at compensation in these cases, on the part of the antagonistic centres, and this is strengthened by voluntary effort, so that considerable strain is made to counteract the tendency to displacement.

This is also seen to a certain extent when the irritation is applied to the cerebellum itself in man and animals, for when irritation of the right side of the cerebellum causes the head and eyes to incline to the side of the anode, there is always some degree of antagonistic or compensatory action on the part of the other cerebellar hemisphere, as shown particularly by reflux oscillations of the eyeballs and efforts to keep the eyes towards the side of the kathode. This may in part also be due to voluntary effort, as in these experiments the influence of the cerebral hemispheres is not excluded, and, in such cases, conscious modifications may coincide with cerebellar action. Hence it is that irritation of one side of the cerebellum causes the feeling of rotation towards, or loss of support on, the other side, because as the action which is called forth is in reality the mechanism to counteract such displacement, the two become indissolubly associated in consciousness, and the one effect invariably calls up the other. The feeling of loss of support in the opposite side of the body may be regarded as analogous to the apparent vanishing of objects in the same direction.

When the various factors concerned in the mechanism of equilibration cannot be brought in usual harmony with each other, vertigo and loss of equilibrium is the necessary result. As labyrinthine impressions form such an essential factor in this mechanism, such relations as have been shown by anatomical investigation to exist between the auditory nerve and the cerebellum derive an important significance.

It is not improbable that this connection may serve to explain, as has been suggested by Hughlings-Jackson, and also by Wundt, how rhythmical pulses on the auditory nerve tend to induce corresponding rhythm in the bodily movements.

§ 46. We have next to consider what relations, if any, subsist between the cerebellum and the eyes. That destruction of the cerebellum does not destroy the sense of sight, is a fact which is clearly demonstrated by Flourens' experiments, and amply confirmed by those of other physiologists. Animals in which the cerebellum has been destroyed evidently see and appreciate threatened violence, and endeavour to escape, but owing to the loss of equilibration their efforts end only in confusion. It will be demonstrated below that the sense of sight is a function of the cerebral hemispheres (§ 65).

Blindness, however, is not an unfrequent result of cerebellar disease, but there is no reason to found any causal relation between the two phenomena. Blindness has been observed chiefly in connection with tumours of the cerebellum; but tumours in any part of the encephalon may produce the same result. The natural tendency of all tumours within the cranial cavity is to increase the intracranial pressure and to obstruct the return of venous blood from the retina. This leads to choking of the optic discs; a condition which ends in atrophy of the optic nerve, and consequent blindness. This effect is explicable, therefore, on purely mechanical grounds, and has no special relation to cerebellar disease.

Though the cerebellum does not seem essential to the sense of sight, yet that it has intimate relations to the optic and oculo-motor nerves, is shown by the importance of visual impressions in the mechanism of equilibration, and by the relation between oculo-motor and general motor adjustments which has been demonstrated by the above experiments. Anatomical investigation has not conclusively established any direct connection between the optic nerves and the cerebellum, though a possible medium of communication may exist, either in the superior peduncles of the cerebellum, or in the valve of Vieussens, which is a direct continuation of the cerebellum into the corpora quadrigemina.

This structure attains a much greater development in fishes and reptiles, and through this the cerebellum forms an integral part of the optic lobes.

It is perhaps owing to this more intimate union of the cerebellum with the optic lobes, that the removal of the rudimentary cerebellum in frogs exercises comparatively little influence on the powers of equilibration.

Whether the connection between the eyes and cerebellum is direct or crossed cannot at present be decided anatomically, but the fact that irritation of the cerebellum causes contraction of the pupil more particularly on the same side, furnishes grounds for believing that the relation between the eye and cerebellum is direct, and therefore that in this respect also cross-relations exist between the cerebellar and cerebral hemispheres.

It has been seen that lesions of the optic lobes also cause disorders of equilibrium, but this does not necessarily imply that the optic lobes are centres of equilibration; for such disturbances must necessarily ensue upon lesions of any of the factors concerned in the mechanism, whether afferent, central, or efferent; and it is obvious that lesions of the optic lobes must interrupt the connections between the optic and ocular nerves and cerebellum, and also destroy the paths and centres of motor co-ordination. The functions of the cerebellum in respect of equilibration cannot be detached from the optic lobes and pons Varolii.

Reasons have been adduced for regarding these especially as the centres of locomotor co-ordination. Lesions of this part of the encephalon must necessarily destroy the apparatus through and by which the cerebellum effects the motor adjustments of equilibration ; and hence, though we regard the cerebellum as the centre in which certain afferent impressions are correlated with these motor adjustments, we must take the cerebellum, optic lobes, and pons Varolii, as together forming a conjoint mechanism, incapable of being disjoined without causing general disorder of function. For though the faculty of co-ordinated progression may be retained notwithstanding the destruction of the cerebellum, yet the loss of equilibration practically renders it impossible ; but if the faculty of locomotor co-ordination is destroyed by lesion of the optic lobes and pons, equilibration must necessarily be rendered impossible. The centre may remain intact, but its afferent and efferent factors are either wholly or partially interrupted or annihilated.

The lateral peduncles of the cerebellum, or *processus a cerebello ad pontem* form the great medium of connection between the cerebellum and the centrifugal or motor tracts. These peduncles decussate in the pons Varolii, and become connected with the motor tracts of the opposite side. As the motor tracts undergo decussation at the lower anterior part of the medulla oblongata, the lateral lobes of the cerebellum are necessarily brought into relation with the muscles on the same side of the body. This anatomical disposition of the lateral peduncles of the cerebellum is in harmony with the results of physiological experiment, for it has been shown experimentally that the movements excited by electrical stimulation occur on the same side. This fact is further well brought out by similar experiments on the brain of fishes and pigeons.

What the signification may be of certain other phenomena which I have described as occurring in connection with irritation of the cerebellum, such as dilatation of the nostrils, I am unable to determine. It is a question whether along with tactile, auditory and visual impressions, other sensory impressions are correlated in the cerebellum with the motor adjustments necessary to space co-ordination. On this point I have no experimental data to go upon.

As to visceral impressions, however, I have already (§ 26) adduced some facts which render it probable that they have an intimate relation to the centres of equilibration, and that abnormal conditions of the one act and react on the other.

§ 47. While I have not considered it necessary to examine and discuss every hypothesis that has been advanced respecting the functions of the cerebellum, no essay on the functions of this part of the encephalon would be regarded as satisfactory, which did not take some notice of the theory propounded by Gall, that the cerebellum is the seat of the instinct of propagation or the sexual appetite. Various facts of clinical observation, comparative anatomy and experimental physiology have been appealed to by those who support this hypothesis. Experimental physiology, however, is altogether opposed to it. Removal of the cerebral hemispheres annihilates all the instincts of self-preservation, and reduces the animal to the condition of a machine, and it would certainly be strange if the instinct of propagation should survive the general ruin of every other form of psychical activity. The positive effects have already been fully discussed.

I have failed to observe, though carefully looking for, any indication of excitement of the generative organs in monkeys or other animals, male or female, during irritation of the median or lateral lobes of the cerebellum.

A cogent argument against the localisation in the cerebellum of the instinct of propagation is furnished by an experiment of Flourens on a cock, the half of whose cerebellum he had destroyed :—

'Cet animal, réduit à la moitié à peu prés de son cervelet, avait été mis plusieurs fois avec des poules, et il avait toujours cherché à les côcher. Chose remarquable, il voulait côcher ces poules, mais il ne pouvait y réussir, parce que, faute d'équilibre, il ne pouvait parvenir à grimper sur leurs dos, et surtout à s'y maintenir . . . . Enfin, et ceci encore n'est pas moins décisif, l'opinion qui a voulu placer dans le cervelet le siége de l'instinct de la propagation, ce coq avait perdu la moitié de son cervelet, et ses testicules étaient énormes' (Flourens, *op. cit.* p. 163, note).

The assertion that there is a constant relation between the development of the cerebellum and the sexual appetite has been so completely refuted by the researches of Leuret ('Anat. Comp. du Syst. Nerv.'); Lelut ('Ann. Med. Psychol.' 1843); John Reid, and Owen ('Comparative Anatomy of the Vertebrates,' vol. i. p. 287) that further consideration of this argument is needless.

The facts of clinical observation and human pathology, on which so much reliance has been placed by those who still cling to Gall's hypothesis, are far from favourable to it.

The girl whose case has been recorded by Combette, in whom the cerebellum was absent, suffered from nymphomania; and a similar case of the co-existence of erotomania with atrophy of the cerebellum, is recorded by Vulpian.

The only indubitable facts of clinical and pathological research, which furnish the slightest justification of Gall's hypothesis, are cases in which disease of the median lobe of the cerebellum has been found to co-exist with priapism or excitement of the generative organs. Cases of this sort led Serres ('Anat. Comp. du Cerveau,' vol. ii.) to modify Gall's view, and to regard the median lobe alone as the seat of the sexual appetite. But these phenomena are capable of a totally different interpretation. The instances in which disease of the cerebellum has co-existed with priapism in the apparent relation of cause and effect, have been chiefly cases of apoplexy or hæmorrhage into the middle lobe, a condition of things eminently calculated to cause irritation of the subjacent posterior surface of the medulla oblongata and pons. While irritation directly applied to the median lobe of the cerebellum produces no vascular turgescence of the generative organs, it has been found by Segalas that irritation of the posterior aspect of the medulla and pons in the region likely to be affected by apoplectic extravasation into the median lobe, produces this effect.

Eckhard ('Beiträge,' vol. vii. p. 67) has likewise shown that the vascular turgescence, which is the immediate cause of erection, may be produced by irritation of the pons, and as high up as the crura cerebri. These facts sufficiently account for the priapism observed in connection with diseases of the middle lobe of the cerebellum, and explain the absence of such effects when the disease occurs in the lateral lobes.

In the opinion of Wundt ('Physiologische Psychologie,' p. 215) the phrenological hypothesis respecting the functions of the cerebellum rests on 'die kritiklose Weise in welcher mangelhaft untersuchte Krankheitsfälle und der Selbst-täuschung dringend verdächtige Beobachtungen zu einem Beweismaterial angehäuft werden.'

According to Longet, with whom I entirely concur, 'Ni la pathologie, ni l'anatomie anormale, ni l'anatomie comparée, ni la physiologie expérimentale ne tendent, par conséquent, à faire admettre le sentiment de Gall sur les fonctions du cervelet' ('Traité de Physiologie,' vol. iii. p. 466).

CHAPTER VII.

FUNCTIONS OF THE CEREBRUM.

Introductory—Method of Investigation.

§ 48. In the preceding chapters we have seen that, notwithstanding the complete removal of the cerebral hemispheres, animals, in proportion to their lowness in the scale, still remain capable of a great variety of most complex and adaptive forms of activity, little if at all differing in character from those prompted by intelligence. On more detailed investigation of these forms of activity, however, the conclusion was arrived at that they were nothing more than responsive actions called into play, through the primary or acquired organisation of the nerve centres, by certain forms of peripherical stimulation, independently of any intelligent adaptation of means to ends on the part of the animal itself. From the facts of human physiology and pathology by which alone the question can be answered, it was concluded that consciousness was inseparable from the activity of the cerebral hemispheres, and that therefore, however much the responsive actions of the lower ganglia might resemble conscious actions, they did not come within the sphere of truly psychical phenomena.

The destruction of the cerebral hemispheres, by annihilating sensation, ideation, volition and intelligence in general, reduces the animal to the condition of a complex machine, the activity of which is the immediate or direct result of certain forms of 'ento-' or 'epi-peripherical' stimulation.

But though the functions of the cerebrum have thus been negatively indicated, the whole mechanism of cerebral activity still remains to be investigated. Though it is by means of the cerebrum that we feel and think and will, the question is whether, by physiological or pathological investigation, we can throw any light on psychological manifestations; whether the cerebrum, as a whole and in each and every part, contains within itself, in some mysterious manner inexplicable by experimental research, the possibilities of every variety of mental activity, or whether certain parts of the brain have determinate functions.

Up to a comparatively recent date, if we except the cumbrous cross-divisions and fanciful localisation of 'faculties' of the phrenological system, the results of experimental physiology and human pathology have been considered as opposed to the localisation of special functions in special regions of the cerebral hemispheres.

The experiments of Flourens, the great pioneer in cerebral physiology, led him to the following conclusions with regard to the question of localisation of function :—

'Ainsi 1°, on peut retrancher, soit par devant, soit par derrière, soit par en haut, soit par côté, une portion assez étendue des lobes cérébraux, sans que leurs fonctions soient perdues. *Une portion assez restrainte de ces lobes suffit donc à l'exercice de leurs fonctions.*

'2°. A mesure que ce retranchement s'opère, toutes les fonctions s'affaiblissent et s'éteignent graduellement ; et passé certaines limites, elles sont tout-à-fait éteintes. Les lobes cérébraux concourent donc par tout leur ensemble à l'exercice plein et entier de leurs fonctions.

'3^{e}. Enfin, dès qu' une perception est perdue, toutes le sont ; dès qu' une faculté disparaît, toutes disparaissent. Il n'y a donc point de siéges divers ni pour les diverses facultés, ni pour les diverses perceptions. La faculté de percevoir, de juger, de vouloir une chose reside dans le même lieu que celle d' en percevoir, d' en juger, d' en vouloir une autre ; et conséquemment cette faculté, essentiellement une, réside essentiellement dans une seule organe' (Flourens, *op. cit.* p. 99).

The views of Flourens, thus so clearly and definitely expressed, have been considered fully borne out by the phenomena observed in connection with disease and injury of the brain in man. There are cases on record in which extensive disorganisation of the brain substance has co-existed with little or no apparent symptoms during life.

Trousseau relates the case of an officer who was shot through the head by a bullet which traversed the anterior part of the brain, and who yet sustained little or no apparent damage bodily or mentally.

Another case, frequently quoted, is that known as the 'American crow-bar case,' the particulars of which are fully reported by Dr. Bigelow, in the 'American Journal of the Medical Sciences' (July 1850). Through an accident in blasting a rock, a young man was hit by a bar of iron, which, entering at the left angle of the jaw, passed clean through the top of his head in the left frontal region, having traversed the anterior part of the left hemisphere. This man speedily recovered, and lived for thirteen years afterwards without manifesting any special symptoms which could be attributed to such a serious injury to the brain.

Numerous other cases might be cited where considerable portions of the brain substance, protruding through fractures of the skull, have been removed by surgeons without causing evil results or apparent mental deficiency.

But the remarkable and frequent coincidence of aphasia, or loss of the faculty of speech, with softening of certain parts of the frontal region of the left hemisphere (vaguely indicated by Bouillaud and Dax, but definitely fixed by Broca in the posterior part of the third frontal convolution, and corroborated by multitudes of since recorded cases), served to render the theory of functional equivalence at least doubtful; though what aphasia really meant in physiological language, or why in symmetrically-formed hemispheres a faculty should be localised in one side to the exclusion of the other, remained a matter of mystery and dispute.

§ 49. The careful clinical and pathological observations in reference to unilateral and localised epileptiform convulsions, and the acute reasonings of the distinguished physician to whom this work is dedicated, throw a new light on the physiological significance of certain parts of the cerebral hemispheres. Hughlings-Jackson pointed out that certain convulsive movements on the one side of the body were due to diseased conditions which caused localised irritation of the opposite cerebral hemisphere. From such facts he came to the conclusion that the convolutions surrounding the corpus striatum had a direct relation to movements; the convulsive phenomena being the result of irritative or 'discharging' lesions of the cortex in this region.

The views of Hughlings-Jackson, published from time to time in the form of scattered contributions to the various medical journals, and now happily being collected by their author ('Clinical and Physiological Researches on the Nervous System'), were regarded by many as ingenious but rather fanciful speculations, and devoid of experimental corroboration, seeing that all experimenters on the brain had failed to produce any such phenomena by irritation of the surface of the cerebral hemispheres.

Like some other parts of the nervous system, the cerebral hemispheres had been found to give no reaction to any form of stimulation applied to them, whether mechanical, chemical, thermal, or even electrical. As regards the first three forms of nerve stimuli, experimenters are still, with one or two notable exceptions, agreed; no reaction being produced by cutting, tearing, burning, or otherwise mechanically injuring the surface. Animals in full consciousness are apparently utterly insensible to all these powerful stimuli of nerves and nerve trunks.

Human beings who have had their brain lacerated or cut, likewise testify to the entire absence of pain or suffering therefrom.

An exception to the agreement among physiologists that mechanical stimuli have no effect on the brain substance, is to be found in certain statements recently made by Nothnagel (Virchow's 'Archiv,' lviii. p. 420). This experimenter states that on injection of a concentrated solution of chromic acid into a circumscribed spot situated on the upper surface of the posterior part of the cerebral hemisphere in the rabbit; or, as he afterwards found, on the simple puncture of this spot with a fine needle, very remarkable results ensue:—the animal suddenly springing away, then suffering from rigidity of the limbs, and soon, in the course of a few minutes, running about as if nothing had happened. These phenomena Nothnagel ascribes to irritation of the substance of the hemisphere. It seems, to say the least, rather an anomalous circumstance, that mechanical irritation of this kind should act only on this part of the brain and not on any other; and when, as we shall find, electrical irritation fails to produce any similar effect when directly applied to the spot alluded to, Nothnagel's statements are to be regarded with grave suspicion. This is strengthened on examination of the exact spot, irritation of which is said to give rise to these remarkable phenomena. The region indicated by Nothnagel lies exactly over the anterior tubercles of the corpora quadrigemina, and the hemispheres at this point form only a comparatively thin lamina. The phenomena described by Nothnagel are just such as result from puncture of these ganglia, as I have determined by exact experiment. I have also ascertained that when the puncture of the posterior part of the hemisphere is carefully confined to the hemisphere itself, and does not descend to the corpora quadrigemina, not the slightest reaction is produced. The lesion of the corpora quadrigemina, caused by a fine needle, may easily escape detection, but yet be amply sufficient to cause all the above-mentioned effects. There can be no doubt, in my opinion, that Nothnagel has fallen into serious error, and his experiments are not of such a kind as to warrant any exception being made to the statement that the cerebral hemispheres are everywhere insensible to mechanical irritation.

In opposition to the generally accepted doctrine, supported by such men as Longet, Majendie, Schiff, etc., that the brain was also insensible to electrical irritation, Fritsch and Hitzig in 1870 (Reichert's und Du Bois Reymond's 'Archiv,' 1870) established, by a series of valuable experiments on dogs, that the direct application of the galvanic current to the surface of the hemispheres in certain regions caused movements; and also the more important fact, that definite muscular contractions were associated with irritation of certain circumscribed areas. Thus they localised centres of movement of the adductors, flexors and extensors of the opposite limbs, as also centres in relation to certain facial and head and neck movements (p. 146). Though vital differences exist between Hitzig and myself in regard to the extent of localisation, and with respect to the true character and significance of these phenomena—the credit of having first experimentally demonstrated the fact of definite localisation belongs to him and his colleague Fritsch, and I regret that in the acrimonious discussions which have arisen in regard to the subject, I have been interpreted as implying otherwise. (See 'Lond. Medical Record,' No. 78, 1874.)

§ 50. The method principally followed by Fritsch and Hitzig in their researches, consisted in applying directly to the surface of the hemispheres, by means of a pair of blunted electrodes, the stimulus of the closing, opening, or commutation of the current of a galvanic pile, of sufficient intensity to cause a distinct sensation when applied to the tip of the tongue. The method employed by myself was the similar application of the electrodes of the secondary spiral of Du Bois Reymond's induction coil, connected with a cell of the mean electro-motive power of 1 Daniell. The resistance in the primary coil was such as to give a current of the maximum of 1·9 units, as estimated for me by my colleague Professor Adams. The induced current generated in the secondary coil at 8 c.m. distance from the primary spiral, was of a strength sufficient to cause a pungent, but quite bearable, sensation when the electrodes were placed on the tip of the tongue. The measurement by the tongue is the most convenient practical test of the intensity of the current, and the best means of regulating the degree of stimulation. In long-continued experiments, the failure of battery power may require closer approximation of the secondary to the primary coil, in order to produce the same sensation on the tongue as at first. Owing to my having given the distance of the secondary from the primary alone in the record of my first experiments, without specially calling attention to this circumstance, it has been concluded by Hitzig and others, that in order to produce the effects I have described, I employed currents of enormous intensity, sufficient to cause structural lesions and unlimited conduction to neighbouring and subjacent parts. I have found by repeated experimentation that, with a uniformly acting cell, and the secondary coil at 8 c.m., all the effects I have described are easily reproducible. Absolute uniformity, however, cannot be secured, on account of the conditions which modify the excitability of the hemispheres.

That which will cause intense and indefinite action in an animal non-narcotised, will excite only moderate and definite action in an animal sufficiently narcotised to abolish all sense of pain, and no effect at all on an animal deeply anæsthetised. Other conditions also mentioned by Hitzig, *viz.*, the state of the circulation in the brain, greatly modify its excitability, hæmorrhage lowering it in a marked degree. Considerable differences also exist in different animals with respect to the excitability of the hemispheres; and it is only rarely that a complete exploration of the brain can be successfully carried out in any one animal, the excitability of the brain rapidly becoming exhausted during the operations necessary to reach the more concealed and deep-seated regions. The skill with which the operations are made considerably affects the degree of success attainable.

In consequence of these various modifying conditions, it is impossible to fix any arbitrary standard, founded on the minimum strength of current necessary to excite any one part in any given subject of experiment. Various regions of the brain differ in regard to their degree of excitability. A current sufficient to cause decided contraction of the orbicularis oculi, will frequently fail to produce any movement of the limbs. By arbitrarily fixing a standard of stimulation which they thought sufficient, Fritsch and Hitzig failed to elicit most important positive results of deep significance, in regions of the brain which they choose to call inexcitable. There is no reason to suppose that one part of the brain is excitable and another not. The question is, how the stimulation manifests itself.

Though it is obviously advisable to use no stronger current than is sufficient to produce a definite result, *the measure of the intensity of the stimulus to be employed in each case is the degree of definite and decided localisation of effects uniformly attainable.* It is also necessary to guard against conduction to neighbouring structures, by insulation of the electrodes, and careful removal of the fluid which is apt to collect on the surface.

The mean strength I have found to be given by the fixation of the secondary coil at 8 c.m., though frequently less and occasionally some increase is required.

The chief object being to secure efficient stimulation, to call forth in a decided and distinct manner the functional activity of the part to which the electrodes are applied, it would matter little whether we used the galvanic or faradic stimulus, provided they were both equally suitable for this purpose. But this is not the case.

Not only a certain intensity, but a certain duration of the stimulus, is necessary to produce the characteristic effect. The closing or opening shock of the galvanic current, applied to the region of the brain, from which movements of the limbs are capable of being excited, causes only a sudden contraction in certain groups of muscles, but fails to call forth the definite purposive combination of muscular contractions, which is the very essence of the reaction, and key to its interpretation. Fritsch and Hitzig, in their description of the results of their experiments with the galvanic stimulus, did not, in my opinion, sufficiently define the true character of the movements. If the galvanic current is applied for a longer period than that necessary to cause the momentary closing or opening shock, electrolytic decomposition of the brain substance ensues at the points of contact with the electrodes; an objection from which the faradic stimulus is entirely free. I have in my possession the brains of monkeys and other animals, on which experimentation by the induced current was maintained for many hours, which, with the exception of some degree of hyperæmia consequent on exposure as much as stimulation, are entirely free from structural lesion.

If the galvanic current is repeatedly closed and opened, an effect resembling the induced current is produced, but with the disadvantage of electrolytic action.

The following experiment will show the comparative efficiency of the galvanic and faradic methods of stimulation:—

Having exposed the brain of a monkey in the region in which I had previously localised the centre of the biceps, excitation of which causes supination and flexion of the forearm, I sought to determine the exact strength of the induced current necessary to produce this definite action, and to compare its effect with that of the galvanic current.

With the single cell already mentioned, and secondary coil at 13 c.m., no result followed; secondary at 12 c.m., likewise without effect; secondary at 11 c.m., slight appearance of outward rotation of the wrist; secondary at 10 c.m., faint supination of the hand; secondary at 9 c.m., gentle and slow supination and flexion of the forearm; secondary at 8 c.m., distinct and decided supination and flexion of the forearm, without any complication with other movements.

The galvanic current was then employed from six cells (small Smee's elements) of Weiss' battery. During closure of the current no result followed, nor when the current was slowly interrupted. With eight cells and slowly repeated interruption, spasmodic and sudden jerks of the hand and forearm were observed, but no definite supination or flexion.

With ten cells and slowly repeated interruption, similar spasmodic movements were caused; but only when the current was rapidly closed and formed, did the spasmodic jerks become converted into the continuous action of supination and flexion of the forearm.

To the tongue the sensation communicated by this stimulus was certainly as strong, if not more pungent, than that of the induced current, and at the point of contact of the electrodes active electrolytic decomposition and evolution of gas began to manifest itself.

This experiment shows that it is not every degree of intensity or every degree of duration of stimulus that is sufficient to excite the due activity of the hemispheres, and that the galvanic method of stimulation is in all respects inferior to that of faradisation. It will be seen also, that the intensity of current derived from the secondary coil at 8 c.m. is not beyond that requisite for the production of distinct and definite reaction.

Leaving for future consideration the significance of the motor phenomena which are manifested on the application of the electrodes to the cortex of the brain, it will be well to consider, in this place, certain objections which have been raised against the view maintained by Hitzig and myself, that the phenomena are the result of excitation of the grey matter of the hemispheres.

§ 51. It has been contended by Dupuy ('Examen de quelques points de la Physiologie du Cerveau,' Paris, 1873) that the movements which are excited by electrisation of the cortex, are in reality due to conduction of the currents to the base of the brain. He shows that extrapolar conduction extends through the brain substance to a considerable distance, and argues that it is impossible to localise the action in the region included within the electrodes. By placing the sciatic nerve of the frog on the posterior part of the brain, and applying the electrodes to the anterior part of the hemisphere, he found that active contraction of the gastrocnemius muscle of the frog resulted, showing that the current had passed along the whole extent of the hemisphere.

The same fact of extrapolar conduction through the brain substance to a considerable distance, has also been more accurately demonstrated by MM. Carville and Duret (' Sur les Fonctions des Hemispheres Cérébraux,' Paris 1875). By placing non-polarisable electrodes on the brain at a distance from the exciting electrodes, and connecting them with a galvanometer, they found that decided deflection of the needle occurred at the moment of stimulation.

Extrapolar conduction through the brain substance is, therefore, a demonstrated fact, and one which *à priori* was to be expected, according to analogy with all other animal tissues.

But the fact of extrapolar conduction is very far from carrying with it the conclusion which Dupuy would draw, that it is to this conduction to the basal ganglia that the movements are due.

The effect of irritation of the basal ganglia is capable of exact estimation. Irritation of the corpus striatum is followed by general contraction of the muscles of the opposite side of the body, and it is impossible, by applying the electrodes directly to the surface of this ganglion, to produce localised contraction in any one muscle or group of muscles.

Irritation of the optic thalamus is altogether negative, no movements of any kind being caused either on the opposite or same side of the body. The effects of electrisation of the corpora quadrigemina, *viz.*, dilatation of the pupils and extension of the trunk and limbs, &c., have already been described.

These positive results, determined by exact experiment, effectually dispose of vague statements respecting the supposed inflence of currents conducted to the basal ganglia.

The phenomena of localised and unilateral convulsive movements, depending, as Hughlings-Jackson shows, on vital irritation of certain regions of the cortex, are essentially of the same nature as those caused by electrisation of the same regions. It can hardly be supposed that vital irritation is capable of conduction to the basal ganglia.

The effects of electrisation of the hemispheres are definite and predictable, and vary with the position of the electrodes. As will be seen in the following chapter, areas in close contact with each other react in a totally different manner. It is incomprehensible why, if the effects are due merely to conduction to the corpus striatum, we should have localised, and not general, contraction of the muscles of the opposite side of the body; and still more incomprehensible why such diverse effects should follow from conduction to practically the same point. There are certain regions of the brain which give no response to electrical stimulation, however strong. The antero-frontal and occipital regions of the brain of the monkey are of this nature. On the theory of conduction the absence of reaction is inexplicable, for these regions are not more distant from the basal ganglia than others which react invariably and uniformly.

A conclusive overthrow of the theory of conduction is the fact that stimulation of the island of Reil, which immediately overlies the corpus striatum (fig. 4, *c*), causes no movements; while the more distant parietal regions at the same time react, actively and definitely, to the same stimulus.

It has further been argued, that if the cortical centres have a motor function the conditions of their excitability ought to be the same as those of motor nerves. As, however, during deep anæsthesia electrisation of the cortex cerebri is without effect, while motor nerves and motor tracts still react actively, it is contended that the hemispheres have no true motor signification. This argument is essentially fallacious, and rebounds with fatal effect on those who adduce it. Under chloroform narcosis the excitability of the nerve centres becomes progressively diminished and abolished from above downwards; the corpora striata remaining excitable when the hemispheres no longer react, and the corpora quadrigemina and crura cerebri remaining excitable when the corpora striata have ceased to respond to stimulation.

If the reactions which follow the application of the electrodes to the surface of the hemisphere are not due to excitation of the grey matter, but to conduction of currents to the basal ganglia and motor tracts, it is unaccountable, if these still remain excitable under deep narcosis, why electrisation of the cortex should cause no movements whatever. The physical conductivity of the brain tissue is not affected by chloroform, and yet the strongest current causes no manifestations. Nothing could show more conclusively that the phenomena are due to functional excitation of the grey matter of the hemispheres, and that complete anæsthesia annihilates their excitability by the electric stimulus.

Carville and Duret, who were at first disposed, with Dupuy, to refer the phenomena to conduction, have, notwithstanding their demonstration of extra-polar conduction, distinctly admitted the possibility of localised stimulation of the cortex, provided that the currents are not excessive. This is entirely in accordance with my own views. But I have already shown that it is not every degree of stimulation which is sufficient to rouse the hemispheres to action. A strength of current sufficient to excite the most violent tetanic spasms, if applied to a motor nerve, has no effect on the cerebral hemispheres. Hence, though conduction may occur, active stimulation will ensue only at the point where the current reaches the necessary degree of intensity, and that is at the point of contact of the electrodes.

The complications which may result from diffusion are not, however, so much from downward conduction to the basal ganglia, as from lateral diffusion and irritation of neighbouring centres and tissues. This constant source of error can only be allowed for and eliminated by carefully-repeated experiments, and with the aid of the complementary method of localised destruction of the centre in question.

Carville and Duret have furnished an interesting confirmation of the fact that electrisation of the cortex does not act by mere conduction to subjacent ganglia or tracts, by an experiment on a dog under very exceptional conditions.

In this animal they failed to produce movements by the application even of the strongest currents to regions which in other animals they had found readily excitable. The cause of this proved to be the existence of a large cavity filled with fluid, occupying the medullary substance of the hemisphere between the cortex and the corpus striatum. Physical conduction from the cortex to the corpus striatum was thus quite perfect, and the connection between the corpus striatum and the cerebral peduncle was intact; yet, owing to the division of the medullary fibres, the cortical centres were unable to communicate their impulse downwards.

It would be quite in harmony with the fact that the movements result from excitation of the cortex, if the same phenomena should be shown to result from irritation directly applied to the cone of medullary fibres which connects each centre with the corpus striatum. For the cortical centres act downwards on the muscles necessarily through the basal ganglia and motor tracts, and the application of the electrodes to the medullary fibres is essentially equivalent to the stimulus caused by the functional activity of the centre itself. That this is actually the case has been demonstrated by Dr. Burdon Sanderson ('Proceed. Roy. Soc.,' June 1874), and also by Carville and Duret. After removal of the grey matter of the cortex in regions from which distinct localised movements could be excited, they found that the application of the electrodes to the denuded medullary fibres caused the same definite action as before, the only difference being, according to Carville and Duret, that the current requires to be intensified.

Putnam ('Lond. Med. Rec.,' 1874), however, found that after carefully severing the connection between the grey matter and the medullary substance, and then closely approximating the cut surfaces, the application of the electrodes failed to produce any result. Here, as Carville and Duret have, I think, rightly indicated, the absence of reaction may have been due to the resistance offered to the current by the accumulation of fluid between the cut surfaces, and to the fact that the stimulus was not of sufficient degree of strength. To deduce from Sanderson's experiments that the cortical centres are not motor, and that the movements in reality depend on the corpus striatum, is no more reasonable than it would be to argue that because the same muscular contractions which result from irritation of the corpus striatum, can also be excited by direct excitation of the crura cerebri or motor columns of the spinal cord, therefore the corpus striatum itself has no motor function.

Such conclusions only indicate a grave misconception of the constitution and evolution of the nerve centres. Essentially the same movements are differently represented in different centres. Many of the muscles concerned in respiration, and reflexly co-ordinated in the medulla oblongata, are also under the control of the will, and centrally represented in the cerebral hemispheres. The motor combinations which are integrated in the corpus striatum, are again differentiated in the cerebral hemispheres, but with essentially different significations.

This re-representation of the same movement in different centres is an important guide to the true interpretation of the facts of the physiology as well as the pathology of the cerebro-spinal system. The highest nerve centres cannot, however, act independently of the lower, nor can the functions of the one be understood out of relation to the other.

With these preliminary considerations on the method of investigation, I will next proceed to describe the phenomena of electrical irritation of the cerebral hemispheres, founded on a repetition and extension of those first published in the 'West Riding Asylum Reports,' vol. iii. 1873. The details of individual experiments are spared, except on points of uncertainty or dispute, reference for these being made to the following Memoirs, presented to the Royal Society:—'Localisation of Function in the Brain,' Croonian Lecture, 1874; 'Abstract, Pro. Roy. Soc.,' 151; 'Experiments on the Brain of Monkeys, First Series, Proceed. Roy. Soc.,' 161, 1875; 'Experiments on the Brain of Monkeys, Second Series, Croonian Lecture, Philosoph. Transactions,' vol. ii. 1875; 'Abstract, in Proceed. Roy. Soc.,' 162, 1875.

The interpretation of the phenomena will be treated of, after the phenomena themselves have been simply described.

CHAPTER VIII.

PHENOMENA OF ELECTRICAL IRRITATION OF THE CEREBRAL HEMISPHERES.

Section I.—*Experiments on Monkeys.*

§ 52. The surface of the cerebral hemispheres in macacques, the species of monkey usually employed in the following experiments, is represented in the accompanying figs. 26, 27. It is divided into lobes and convolutions by certain primary and secondary fissures or sulci. Of the primary fissures there are three, easily distinguished by the letters on the figure. A is the *Fissure of Sylvius*; B is the *Fissure of Rolando*; C is the *Parieto-occipital or Perpendicular Fissure.*

The Frontal Lobe (F L), situated in advance of the fissure of Rolando, is divided by secondary fissures into the following convolutions. F_1, *the Superior Frontal Convolution*; F_2, *Middle Frontal Convolution*; F_3, *Inferior or Third Frontal Convolution.*

These convolutions, separated from each other by two fissures, termed respectively the *Supero-Frontal* (*s f*) and *Infero-Frontal* (*i f*) *Sulci*, join posteriorly what is usually termed the *Ascending Frontal Convolution* (A F), which lies between the fissure of Rolando (B) and the *Antero-Parietal Sulcus* (Huxley) (*a p*). This convolution was not included in the frontal lobe by Gratiolet, who considered the frontal lobe bounded posteriorly by the antero-parietal sulcus, and placed the ascending frontal convolution (Turner) in the parietal lobe, of which it formed the first ascending parietal convolution. For physiological reasons, I think the nomenclature of Gratiolet is preferable to that adopted by Turner, though I have followed the usually accepted divisions.

The inferior aspect of the frontal lobe sometimes receives the name of the *Orbital Lobule* (F O), fig. 27.

The *Parietal Lobe* (P L) extends from the fissure of Rolando (B) to the Parieto-Occipital fissure (C).

Here we distinguish the *Ascending Parietal Convolution* (A P), bounded by the fissure of Rolando in front, and behind by the *Intra-Parietal Fissure* (*i p*). This convolution ends, superiorly, in the *Postero-Parietal Lobule* (Huxley) (P P L), the posterior boundary of which is formed by the Parieto-Occipital fissure (C). The other convolution of the parietal lobe is termed the *Angular Gyrus* (A G), or *pli courbe* (Gratiolet), which bends round the upper extremity of the fissure of Sylvius (A) and superior temporo-sphenoidal fissure (T).

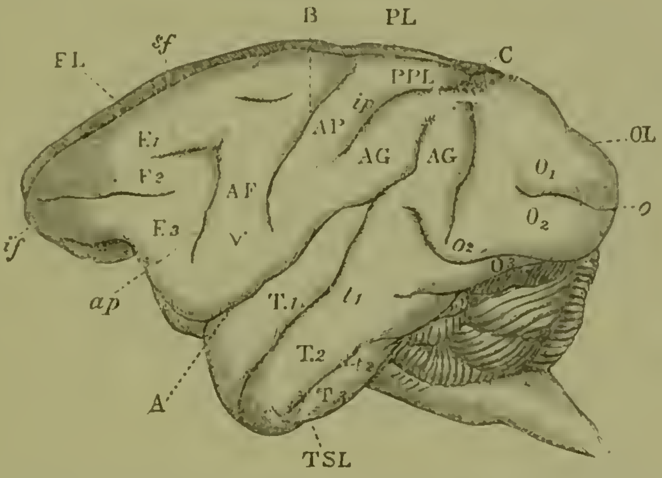


FIG. 26.—Left Hemisphere of the Brain of the Monkey (Macaeque). A. The fissure of Sylvius. B. The fissure of Rolando. C. The parieto-occipital fissure. FL. The frontal lobe. PL. The parietal lobe. OL. The occipital lobe. TSL. The temporo-sphenoidal lobe. F_1. The superior frontal convolution. F_2. The middle frontal convolution. F_3. The inferior frontal convolution. *sf*. The supero-frontal sulcus. *if*. The infero-frontal sulcus. *ap*. The antero-parietal sulcus. AF. The ascending frontal convolution. AP. The ascending parietal convolution. PPL. The postero-parietal lobule. AG. The angular gyrus. *ip*. The intra-parietal sulcus. T_1, T_2, T_3. The superior, middle and inferior temporo-sphenoidal convolutions. t_1, t_2. The superior and inferior temporo-sphenoidal sulci. O_1, O_2, and O_3. The superior, middle and inferior occipital convolutions. o_1 o_2. The first and second occipital fissures.

The *Temporo-Sphenoidal Lobe* (T S L) lies behind and below the fissure of Sylvius. It is divided by secondary fissures (t_1, t_2) into three convolutions—*Superior* (T_1), *Middle* (T_2), and *Inferior* (T_3) *Temporo-Sphenoidal Convolutions.* The upper ends of these convolutions pass into the *Occipital Lobe* (O L). In this, also, three convolutions are distinguished, *viz.*, the *Superior* (O_1), the *Middle* (O_2), and *Inferior* (O_3) *Occipital Convolutions.*

When the lips of the fissure of Sylvius are separated, another lobe is displayed, called the *Central Lobe*, or *Island of Reil* (see fig. 4, *c*), which encloses the extra-ventricular nucleus of the corpus striatum. In the monkey the surface of this lobe is smooth, and not divided, as in man, into convolutions.

On the internal aspect of the hemisphere (fig. 27), are to be distinguished certain fissures and convolutions. The convolution bending round the *Corpus Callosum* (C C) is termed the *Gyrus Fornicatus* (G F), commencing at the frontal extremity of the hemisphere, and passing across the fissure *c f* into the *Uncinate Convolution* (G U) inferiorly and posteriorly. The uncinate convolution at its anterior inferior aspect becomes recurved, so as to form a sort of crochet, and has received the name of the *Crochet* (Gratiolet) or *Subiculum Cornu Ammonis* (S). Separated from the gyrus fornicatus by a fissure termed the *calloso-marginal fissure* (*c m s*), is a convolution which bounds the internal margin of the longitudinal fissure between the two hemispheres. It is termed the *Marginal Convolution* (C M). Between the posterior extremity of the calloso-marginal sulcus, and the internal Parieto-Occipital Fissure (C), an irregularly shaped lobule (Q) has received the name of the *Quadrilateral Lobule* or *Præcuneus*.

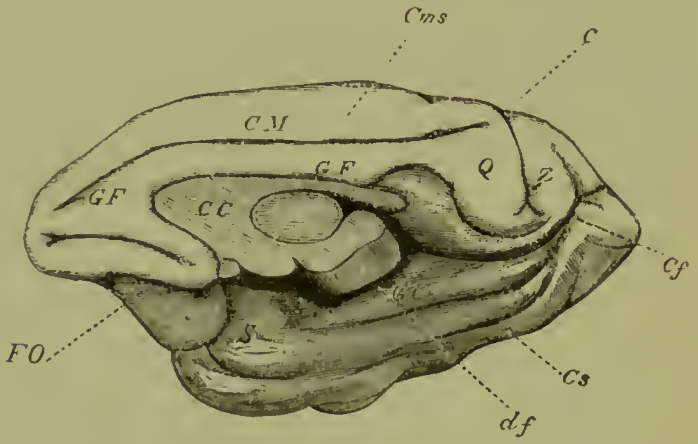


FIG. 27.—The Internal Aspect of the Right Hemisphere of the Monkey (Macacque). CC. The corpus callosum divided. C. The internal parieto-occipital fissure. *cms*. The calloso-marginal fissure. *Cf*. The calcarine fissure. *df*. The dentate fissure. *Cs*. The collateral fissure. GF. The gyrus fornicatus. CM. The marginal convolution. GU. The uncinate convolution. S. The crochet, or subiculum cornu Ammonis. Q. The quadrilateral lobule, or præcuneus. Z. The cuneus. FO. The orbital lobule.

The fissure (*c f*), called the *Calcarine Fissure* (Huxley) marks the position of the hippocampus minor in the interior of the posterior cornu of the lateral ventricle. It is continued in front into the *Dentate Fissure* (*d f*), which marks the position of the hippocampus major in the descending cornu of the lateral ventricle. The uncinate convolution is bounded by this fissure above, and is separated from the inferior temporo-sphenoidal convolution (T_3), fig. 26, by a sulcus called the *Collateral Fissure* (Huxley) (*C s*).

§ 53. The centres of electrical irritation are indicated on the accompanying figures (figs. 28, 29, 30) by areas or circles, which mark the extent of the regions stimulation of which gives rise to certain definite movements. The areas have no exact line of demarcation from each other, and, where they adjoin, stimulation is apt to produce the conjoint effect peculiar to each. This occurs the more readily the greater the intensity of the current employed. The area of limited action is most correctly indicated by the centre of the circle. The boundaries were determined by repeated individual application of the electrodes around these points.

(1.) On the postero-parietal lobule. *Advance of the opposite hind limb*, as in walking. Occasionally the action is limited to the foot and ankle, the foot being flexed on the ankle, and the toes spread out.

(2.) On the upper part of the ascending parietal, and adjoining part of the ascending frontal convolutions. *Complex movements of the thigh, leg and foot*, with adapted movements of the trunk, by which the foot is brought to the middle line of the body, as when the animal grasps anything with its foot, or scratches its chest or abdomen.

Various degrees of this completed action may be observed according to the duration and strength of stimulation, but the full development of the activity of this centre is such as I have described.

(3.) Situated close to the ascending frontal portion of the above centre, and close to a slight sulcus or depression at the upper part of the ascending frontal.

Movements of the tail, generally associated with some of the movements described under the last.

I have not been able to dissociate the two from each other completely. In new-world monkeys this might be possible.

(4.) Situated behind (3) and below (2), and occupying adjacent margins of the ascending frontal and ascending parietal convolutions.

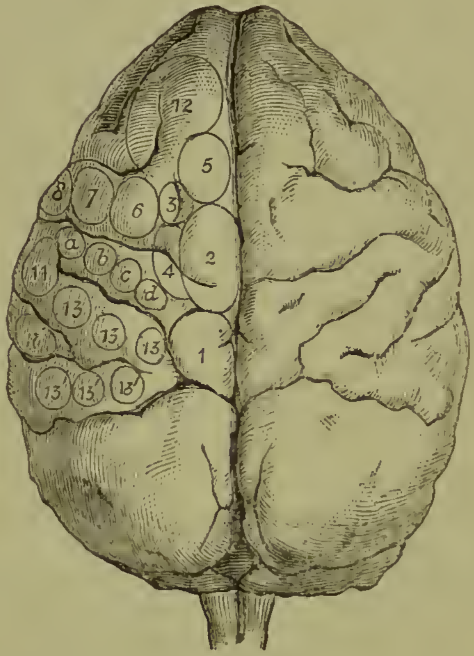


FIG. 28.—Upper Surface of the Hemispheres of the Monkey. (Roy. Soc.)
The circles and included numerals are explained in the text.

Retraction with adduction of the opposite arm, the palm of the hand being directed backwards.

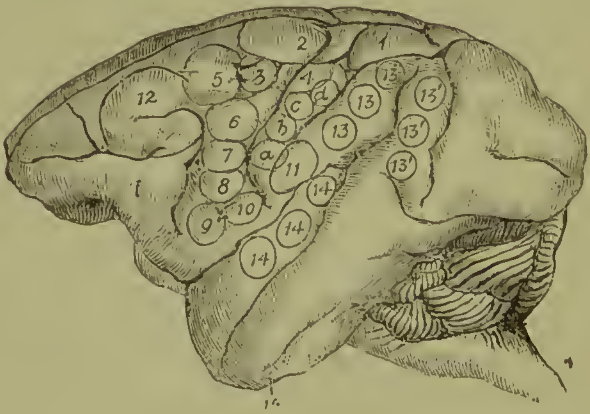


FIG. 29.—The Left Hemisphere of the Monkey. (Roy. Soc.)
The circles and numerals have the same signification as in last figure.

This action, resembling a swimming movement, is such as may be ascribed to the latissimus dorsi.

(5.) On the ascending frontal convolution, at its junction with superior frontal.

Extension forward of the opposite arm and hand, as if to reach or touch something in front.

Circles (a), (b), (c), (d), placed on the ascending parietal convolution.

Individual and combined movements of the fingers and wrist, ending in clenching of the fist. Centres for the extensors and flexors of the individual digits could not be differentiated, but the *prehensile movements* of the opposite hand are evidently centralised here.

(6.) In the ascending frontal convolution at the bend or knee of the antero-parietal sulcus.

Supination and flexion of the forearm, by which the hand is raised towards the mouth.

This action is apt to be associated with the following.

(7.) On the ascending frontal convolution, below last circle.

Action of the zygomatics, by which the angle of the mouth is retracted and elevated.

(8.) On the ascending frontal below last circle.

Elevation of the ala of the nose and upper lip, with depression of the lower lip, so as to expose the canine teeth on the opposite side.

(9) and (10). Situated at the inferior extremity of the ascending frontal, on a level with the posterior termination of the third frontal convolution.

Opening of the mouth, with protrusion (9) *and retraction* (10) *of the tongue.* Alternate opening and closure of the mouth, with movements of the tongue, frequently continue for some time after the electrodes are withdrawn. In this case the movements are distinctly carried out bilaterally.

(11.) Extending from (10) to the lower extremity of the ascending parietal convolution.

Retraction of the opposite angle of the mouth. The platysma myoides is thrown into action, and when this is powerful the head is drawn slightly to the side.

(12.) Situated on the posterior half of the superior and middle frontal convolutions.

The eyes open widely, the pupils dilate, and head and eyes turn towards the opposite side.

(13) and (13′) placed on the anterior and posterior limbs of the angular gyrus (*pli courbe*) respectively.

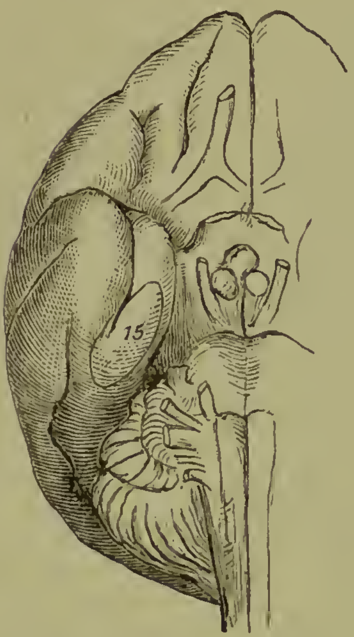


Fig. 30.—Base of the Brain (right side) of the Monkey. (Roy. Soc.)

The eyes move towards the opposite side, with an *upward* or *downward* deviation, according as the electrodes are on 13 or 13′.

The pupils also generally become contracted, and there is a tendency to closure of the eyelids as if under the stimulus of a strong light.

The head frequently follows the direction of the ocular movements, though this is not always observed.

(14.) Placed on the superior temporo-sphenoidal convolution.

Pricking of the opposite ear, head and eyes turn to the opposite side, pupils dilate widely.

(15.) Subiculum cornu Ammonis, or lower and inner aspect of the temporo-sphenoidal lobe (fig. 30).

Torsion of the lip and nostril on the same side, so as to cause a partial closure of the nostril, as when a pungent odour is applied.

No definite or constant results follow stimulation of other parts of the brain, but the following phenomena have been observed:—

Lower extremity of the middle temporo-sphenoidal convolution.

Stimulation of this in a few cases caused movements of the tongue, cheek-pouches and jaws, such as might be caused by some sapid stimulus in the mouth.

Frontal lobes, including all in advance of circle (12) and the inferior frontal and orbital regions.

Results in general, negative. In one case stimulation of the antero-frontal region was associated with rolling of the eyes to the opposite side. Beyond this, which may have been a mere coincidence, no effect was caused by stimulation of this region.

Island of Reil—Central Lobe.

The result in this case is also negative.

Occipital Lobes.

Stimulation of these is likewise without apparent effect.

In one case I observed, that on insinuating the electrodes towards the inner aspect of the inferior occipital convolution, apparent uneasiness was caused, as exhibited in restless movements of the hind legs and tail. Whether these were due to conduction of the current to the dura mater or tentorium, or to direct stimulation of the upper end of the uncinate gyrus, could not be determined. Experimentation in this region is extremely difficult, and sources of fallacy numerous, it being impossible to be quite certain of the localisation of the stimulus.

Marginal Convolution (fig. 27, *C M*).

This was explored in one case only, in which it was found that irritation of this convolution in the parieto-frontal region gave rise to movements of the head and limbs, apparently similar to those already obtained by stimulation of the corresponding regions on the external surface.

Gyrus Fornicatus (fig. 27, *G F*).

Stimulation of this by slipping the insulated electrodes deeply into the longitudinal fissure, failed to produce any outward manifestation.

Corpus Callosum (fig. 27, *C C*).

Stimulation of this is also without effect.

SECTION II.—*Experiments on Dogs.*

§ 54. In the brain of the dog (fig. 32) there are two fissures of primary importance, *viz.*, the *fissure of Sylvius* (*A*), and the *crucial sulcus* (*B*), or *sillon crucial* (Leuret), termed by Owen the *frontal sulcus.* Besides these there are certain sulci which have a general direction from before backwards, which divide the surface into four convolutions, termed by Leuret, the *external convolutions.*

The first of these, the *First External Convolution* (fig. 32, I.) forms a bend round the crucial sulcus, constituting what I have termed the *Sigmoid Gyrus*, adopting a name employed by Mr. Flower in his description of the brain of the Proteles ('Proc. Zool. Soc. Lond.,' Nov. 1869).

The *Second External Convolution* (fig. 32, II.) pursues a course from before backwards parallel to the above-mentioned, and at its posterior third is divided into two limbs by a secondary fissure.

The *Third External Convolution* (fig. 32, III.) pursues a similar direction.

The *Fourth External Convolution* (fig. 32, IV.) arches over the fissure of Sylvius. I have sometimes termed it the Sylvian convolution. Towards the frontal and orbital aspect of the hemisphere, the continuity of the individual external convolutions becomes obscure and indefinite. (See fig. 32.) The electrical excitability of the brain, and the fact of localisation, were first demonstrated on the brain of dogs by the important researches of Fritsch and Hitzig in 1870. ('Reichert und Du Bois-Reymond's Archiv,' 1870, Heft 3.) The following extract and accompanying figure (fig. 31) are from the original description of the results arrived at by Fritsch and Hitzig, prior to the localisation experiments on various animals described in this chapter.

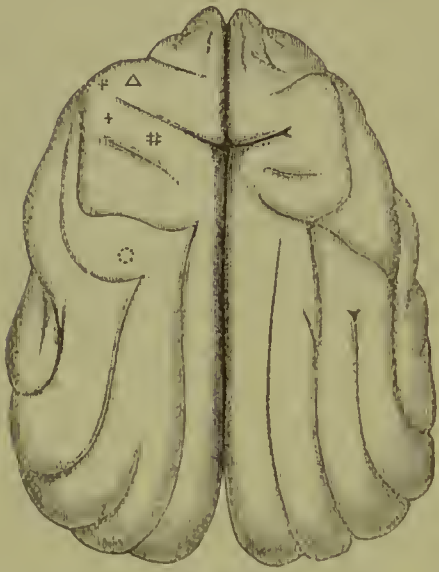


FIG. 31.—Figure of the Brain of the Dog, illustrating Fritsch and Hitzig's researches.

'The centre for the neck-muscles (fig. 31, △) lies in the lateral part of the pre-frontal gyrus, at the point where the surface of this convolution abruptly descends. The outermost extremity of the post-frontal gyrus contains, in the neighbourhood of the lateral end of the frontal fissure (fig. 31, ÷), the centre for the extensors and adductors of the fore-limb. Somewhat behind the same, and nearer the coronal fissure (fig. 31, +) lie the ruling centres for the flexion and rotation of the limb. The centre for the hind leg (fig. 31, ‡‡) is also found in the post-frontal gyrus, but nearer the middle line than that of the fore-leg, and somewhat further back. The facial (fig. 31, ◌) is innervated from the middle part of the supersylvian gyrus. This region generally has an extension of over 0·5 centimetre, and stretches before and behind the bend over the Sylvian fissure. We must add, that we did not always succeed in setting the neck-muscles in action from the first-mentioned point. The muscles of the back, tail and abdomen we have often enough excited to contraction from points lying between those marked, but no circumscribed point from which they could be individually stimulated could be satisfactorily determined.

'The whole of the convexity lying behind the facial centre we found absolutely unexcitable, even with altogether disproportionate intensity of current.' (*Op. cit.*, reprinted in 'Untersuchungen über das Gehirn,' by E. Hitzig, Berlin, 1874.)

Hitzig, in subsequent experiments ('Untersuch ü. das Gehirn,' chap. iii.), while confirming in many respects the results described by me in the 'West Riding Asylum Reports,' vol. iii., questions the validity of others, especially as regards the excitability of the regions posterior to the fissure of Sylvius. The phenomena described by me he attributes to vague conduction of currents. In support of his view, he endeavours to show that the phenomena are discordant with each other, and that my experiments would localise different motor centres in essentially the same regions, and motor centres for the same movements in widely-different parts of the brain. These discrepancies which Hitzig discovers do not exist in reality, but only in his own method of reading the facts. The mere fact that movements result from stimulation of a given part of the hemisphere does not necessarily imply that the same is a motor centre in the proper sense of the term. It will afterwards be shown that the movements which result from stimulation of the regions in question, are expressive of sensation, and that the character of the movements furnishes an important index to the nature of the sensation.

The movements, therefore, being of the character of associated or reflex indications of sensation, will vary in extent according to the degree of excitability of the sensory centres. Hence apparently different effects may easily be seen to be essentially only degrees of the same reaction. Thus, in one case a movement of the eyeballs or of the ear may be observed; in another this may be associated with turning the head to the opposite side. But this does not imply that in the one case I describe a motor centre for the eyeballs, and in another in the same region a motor centre of the muscles of the neck. In some cases, again, movements may be excited by stimulation of a sensory centre, apparently the same as those which result from stimulation of a truly motor centre. An instance of this will be seen on comparing the effects of stimulation of (12) in the brain of the monkey, with those caused by stimulation of (14). The signification, however, is widely different in the two cases.

In the following description, with the exception of details of experiment, the results agree in all essential respects with those which I first published. But certain phenomena, the signification of which I had not been able clearly to interpret, and therefore regarded as doubtful and in need of further investigation, I am now inclined to attribute to conduction of currents hardly possible to avoid, owing to the extreme difficulty of clearly exposing and isolating the region in question. This is so especially in the case of exploration of the frontal extremity of the brain of the dog, cat, etc., which is difficult of exposure, and is in immediate relation to the large olfactory bulb of these animals. I described certain sudden movements of the head, and sometimes of the respiratory muscles, as resulting from the application of the electrodes in the antero-frontal regions. These, I think, are to be ascribed—and in this I quite agree with Hitzig—to conduction of the current to the sensitive olfactory bulb or dura mater, the movements being merely reflex phenomena. The difficulties of localisation necessarily increase when the regions of the brain under exploration are incapable of being clearly freed from surrounding sensitive structures ; and where such is the case the phenomena must be regarded as of doubtful significance unless their nature can be resolved by other and complementary methods of investigation.

In the following description, in order to facilitate comparison with the results of similar experiments on the brain of the monkey, the same numbers are placed on corresponding regions. They do not pretend to indicate more than approximate physiological homologies, certain individual peculiarities being observable in different animals which scarcely admit of strict comparison with each other.

The references are to fig. 32.

(1) *The opposite hind leg is advanced as in walking.*

There is no movement of the dog's leg which can be compared to that resulting from (2) in the brain of the monkey.

(3) *Lateral or wagging motion of the tail.*

In my first experiments ('West Riding Reports,' vol. iii. fig. 6) the position of the centre was not accurately enough defined, the circle (9) being placed farther back on the woodcut than it should have been. In the case in question, the stimulation of the tail movements from so extended an area was no doubt due to a condition of hyper-excitability caused by repeated exploration. Subsequent experiments led to more exact definition and limitation of the area, as indicated in figure 32.

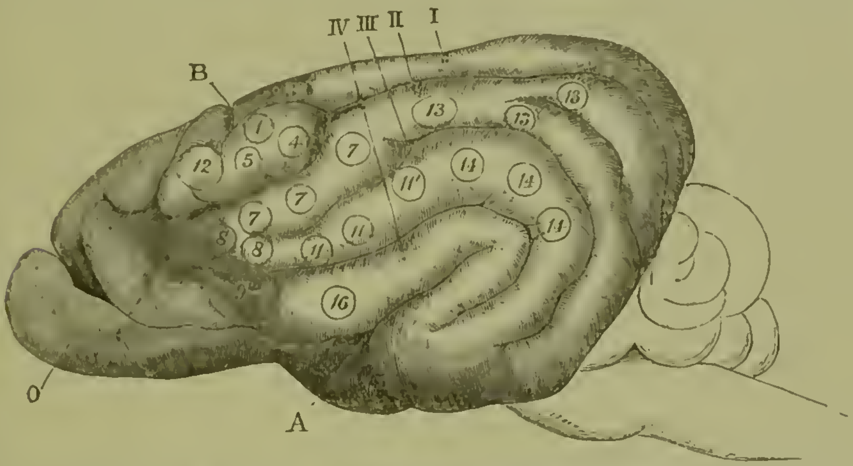


FIG. 32.—Left Hemisphere of the Brain of Dog. A. The fissure of Sylvius. B. The crucial sulcus. O. The olfactory bulb. I, II, III, IV, indicate the first, second, third and fourth external convolutions respectively. The circles and numerals are explained in the text. (1), (4), and (5) are on the *Sigmoid* gyrus.

(4) *Retraction and adduction of the opposite fore-limb.*

(5) *Elevation of the shoulder and extension forwards of the opposite fore-limb,* as in the act of stepping forwards.

(+) The centres (6) and those marked (*a*, *b*, *c*, *d*) in the brain of the monkey are not, as far as I have found, differentiated in the brain of the dog, but occasionally flexion of the paw is joined with the movements described under circles (4) and (5) In one case (a large retriever dog with large brain), I found that stimulation of (+) caused flexion of the paw independently of other movements.

(7) Placed on various points in the frontal division of the second external convolution.

Conjoint action of the orbicularis oculi and zygomatics, causing closure of the opposite eye. At the same time the eyeballs are seen to move if the eye be forcibly kept open. The movement of the eyeballs I have found to be divergent, and associated with contraction of the pupils. Hitzig, also, has observed movements of the eyeballs on stimulation of this region.

(8) Situated at the anterior conjoint extremity of the second and third external convolutions.

Retraction and elevation of the opposite angle of the mouth, so as partially to open the mouth.

(9) This may be taken to correspond with circles (9) and (10) in the monkey.

The mouth is opened and the tongue moved, being alternately protruded and retracted. Bilateral action.

Occasionally, as described in my first experiments, the stimulation of this region caused also vocalisation, or feeble attempts at barking or growling. In a subsequent experiment this was exhibited in a very striking manner. Each time the electrodes were applied to this region, the animal uttered a loud and distinct bark. To exclude the possibility of mere coincidence, I then stimulated in succession various parts of the exposed hemisphere, producing the characteristic reaction of each centre, but no barking.

The reapplication of the electrodes to the mouth centre elicited the barking, and did so invariably several times in succession.

(11) The essential action seems to be *retraction of the angle of the mouth* from action of the platysma. Occasionally, especially near the frontal extremity, I have observed the angle of the mouth retracted on both sides, and on one or two occasions I have observed the ear on the opposite side drawn forwards while the angle of the mouth was retracted. This seems to be only an intenser form of essentially the same muscular action.

At the point marked (11′) the action is rather elevation of the angle of the mouth and side of the face, so as to cause closure of the eye. In this respect it resembles the action of (7).

(12) *Opening of the eyes, and dilatation of the pupils; the eyes and then the head turning to the opposite side.*

In one or two cases I have observed inward or convergent movement of the eyeballs, the pupils, however, being always dilated.

This action is characteristic of the anterior division of the sigmoid gyrus, and is evidently homologous with (12) in the brain of the monkey.

(13) *The eyeballs move to the opposite side*, generally with some degree of diagonal deviation, the pupils occasionally being contracted, and the eyes tending to close, though if already closed there may be a slight opening at the moment of stimulation. In several experiments the head was observed on continued stimulation to move in the same direction as the eyes.

(14) *Pricking, or sudden retraction, of the opposite ear.*

I have not observed the association of this with the action of (12), as is so constantly the case on stimulation of (14) in the monkey.

(15) *Torsion of the nostril on the same side*, as if from irritation directly applied to it.

Stimulation of other regions of the brain does not give always very definite or distinctly differentiated results.

On stimulation of the frontal division of the fourth external convolution (16), I have on one or two occasions observed movements which may be characterised as elevation of the lip and dilatation of the nostrils; but whether these are due to localised irritation of this region, or rather to be ascribed to irritation of the olfactory tract, it is exceedingly difficult to determine.

Irritation of the frontal extremity of the brain, as I have already intimated (p. 148), sometimes causes irregular and sudden movements of the head or of the respiratory muscles; but these results are, I believe, really due to irritation of the dura mater or of the olfactory bulb, which lies in such close proximity.

The posterior limb of the Sylvian or lower external convolution gives no definite reaction, as far as I have been able to determine. Irritation of the posterior division of the superior external convolution, and of the regions posterior to the points marked, has not yielded very constant results, though occasionally I have observed indications of restlessness or movements which might be taken as signs of painful cutaneous stimulation. Experiments on a corresponding region in the brain of the cat, as will be seen below, give similar results. In themselves these facts are not sufficient to carry any conclusions as to the probable functions of this region, but they are important when taken in connection with other phenomena (see § 67).

Experiments on Jackals.

§ 55. The following experiments on two wild North African jackals (*Canis aureus*), which I obtained through Mr. Bartlett, superintendent of the Zoological Society's Gardens, may be taken as equivalent to those on dogs, on account of the close resemblance between these animals as to habits and as to configuration of brain (fig. 33).

(1) *Advance of the opposite hind leg* from its extended position.

(3) Some *movements of tail*, observed in the one case.

(4) *Retraction of the opposite fore-leg.* In the one case this was combined with adduction, in the other the humerus was retracted and the fore-arm flexed.

(5) *Elevation of the shoulder, with flexion of the fore-arm and paw.* This was followed by sudden extension forward. Individual centres for flexion and extension could not be differentiated in either case.

(7) *Elevation of the cheek and partial closure of the eye.* At (7′) *closure of the eye* was especially produced. The eyeballs in the one case were observed to diverge. The condition of the pupils was not noted.

(8) *The upper lip elevated and the teeth displayed*, but the mouth not completely opened.

(9) *The mouth opened and the tongue protruded.* No vocalisation was observed in either case.

(11) Various points on the frontal division of the third external convolution. The *angle of the mouth strongly retracted*, the platysma being in action.

(12) *Both eyes widely opened*, *the pupils dilated*, *the eyes turned to the opposite side*, *the head ultimately turning in the*

same direction. In the one case the eyeballs were converged, and the ears pricked up, so as to give the appearance of earnest attention.

At the anterior aspect of the same sigmoid gyrus, marked by the circle (12′), along with the wide opening of the eyes and dilatation of the pupils the head was lowered, and the muzzle directed to the shoulder of the same side, owing to contraction of the opposite sterno-mastoid.

The conjoint action of both sides would cause the appearance of an animal 'pointing' at game.

(13) In the one case, and only partially explored, the stimulation of (13) caused the *head to be directed to the opposite side*, and with it the ear was pricked up, but the eyes were not observed. The pricking of the ear was like that resulting from stimulation of (14), and may have been due to a complication of the irritation of (13) with (14).

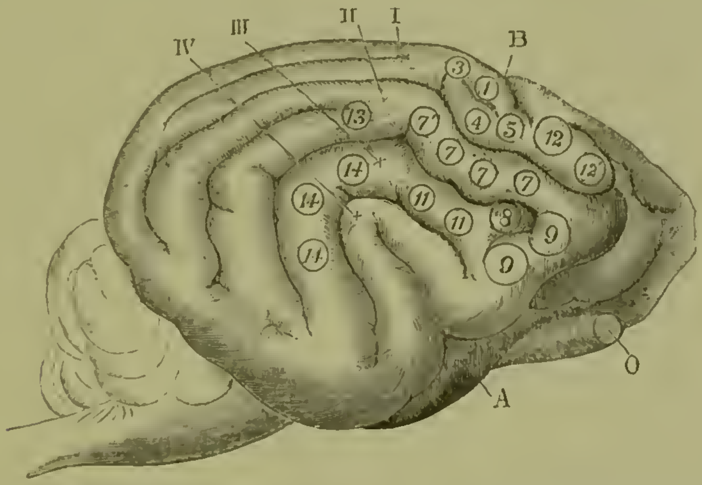


FIG. 33.—Right Hemisphere of the Brain of the Jackal. A. Fissure of Sylvius. B. Crucial sulcus. I. Superior external convolution. II. Second external convolution. III. Third external convolution. IV. Fourth external convolution. The signification of the circles and numerals is given in the text.

(14) *Sudden retraction or pricking of the opposite ear.* On one or two occasions the application of the electrodes in this region caused the animal to make a sudden spring or bound forward, pricking up both ears, as if suddenly startled.

Further experiments were not made on these animals, except in reference to the excitability of the posterior or recurved portion of the superior external convolution. In the one case no results were observed. In the other, signs of uneasiness were caused, shown in kicking with opposite hind leg, and turning of the head backwards as if to ascertain the cause of irritation.

In this respect the experiment agrees with a similar observation in the dog, and, as will be seen also, in the cat.

Section III.—*Experiments on Cats.*

§ 56. In the brain of the cat the convolutions are disposed in a manner similar to those of the brain of the dog and jackal.

The appearance of the brain is represented in the accompanying figures (figs. 34, 35), the one giving a surface view of both hemispheres, the other representing the left hemisphere.

Fig. 34.—Upper Surface of the Hemispheres of the Cat. B. The crucial sulcus.

The *Fissure of Sylvius* (A) and the *Crucial Sulcus* (figs. 34, 35, B) are easily recognised.

The *First External Convolution* makes a sigmoid curve round the crucial sulcus, less complex than the corresponding gyrus of the dog's brain. The *Second External* (fig. 35 II.) runs parallel with the first, fusing with it posteriorly.

The *Third External* (fig. 35 III.) is connected by a bridging or *Annectent Gyrus* with the *Fourth* or *Sylvian Convolution*, which arches over the upper extremity of the fissure of Sylvius. The numeral (III.) is placed on the annectant gyrus, while IV. indicates the fourth external, or Sylvian, convolution.

(1) *Advance of the opposite hind-leg*, as in walking.

(4) *Retraction and adduction of the fore-leg.* Rapidly performed, the movement is such as the cat makes when striking a ball with its paw.

(5) *Elevation of the shoulder and upper arm*, while the fore-arm and paw are maintained in a semi-flexed condition. The movement is like that of raising the paw to step forward as in walking.

It would seem as if both (5) and (6) in the monkey were represented in this movement.

(*a*) *A clutching action of the paw, with protrusion of the claws.* This is one of the most characteristic movements of the cat, and is readily called into action. It may be compared, as indicated by (*a*), with the clenching of the fist, caused by stimulation of the ascending parietal convolution in the monkey. The action is frequently associated with that of the following centre.

(7) Various points on the second external convolution, frontal division.

Elevation of the angle of the mouth and cheek, with closure of the eye.

The state of the eyeballs and pupils was not observed in all cases, though movements of the eyeballs were observed in some.

Hitzig has also observed movements of the eyeballs, as in the case of dogs, from irritation of this region.

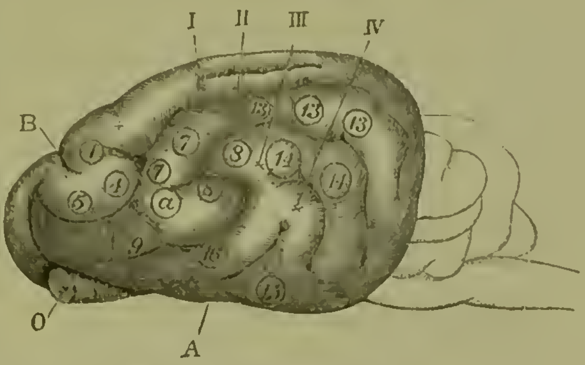


FIG. 35.—Left Hemisphere of the Brain of the Cat. A. The fissure of Sylvius. B. The crucial sulcus. O. The olfactory tract, cut. I. The superior external convolution. II. The second external convolution. III. The third external convolution. IV. The fourth external convolution.

(8) *A combination of retraction with some degree of elevation of the angle of the mouth, and drawing downwards and forwards of the ear.*

Occasionally the movement of the ear alone is caused.

(9) A region including the anterior and orbital extremity of the conjoint lower external convolutions.

Opening of the mouth and movements of the tongue.

Frequently this was associated with vocalisation, and other expressional actions, such as spitting, and lashing the tail as if in rage.

I have not been able to differentiate any centre corresponding to (11) in the dog, giving uncomplicated action of the platysma. It seems to be associated with the movements described under (8).

Nor have I succeeded in determining a centre corresponding to (12) in the monkey, dog and jackal, or one corresponding to (3), the tail centre of the dog.

Stimulation of the region (+), just posterior to the sigmoid gyrus, which anatomically might be expected to correspond to the tail centre of the dog, was either negative, or occasionally, on strong stimulation, attended by movements of the eyes and turning of the head to the opposite side—effects, I think, to be ascribed to lateral diffusion to the following region.

(13) Various points on the parietal aspect of the second external convolution.

The eyes move to the opposite side, and frequently the head turns in the same direction. The pupils were occasionally observed to contract.

(14) *The ear is suddenly retracted or pricked, and the head and eyes directed to the opposite side.*

Sometimes the ear alone is moved, and when the narcosis is deep or the animal much exhausted, no result is produced by stimulation.

(15) The tip of the uncinate convolution.

Elevation of the lip and torsion of the nostril on the same side as from irritation of the nostril.

(16) Situated at the frontal extremity of the lower external or Sylvian convolution.

Divergence of the lips so as partially to open the mouth, which becomes fully opened when the stimulation is kept up.

In my first paper in the 'West Riding Reports,' I described certain sudden movements of the head as resulting from stimulation of the frontal extremity of the hemispheres. These I am inclined to attribute to conduction of the current to the olfactory bulb, irritation of which can scarcely be guarded against in experimentation on this deeply-seated part.

Irritation of the posterior limb of the Sylvian convolution very frequently caused movements of the jaws, generally closure, a result of doubtful significance owing to the proximity of this region to the cut surface of the temporal muscle, which requires to be reflected in order to expose it clearly. Other considerations, however, to be adduced in the next chapter, render it not improbable that the movements are of a reflex nature, due to stimulation of a sensory centre situated in or near this region.

In some experiments, just as in dogs and jackals, stimulation of the recurved portion of the superior external convolution caused signs of uneasiness, as if from pain or irritation referred to the opposite extremities, perhaps indicating the stimulation of a centre of tactile sensibility. On this subject see below (§ 67).

SECTION IV.—*Experiments on Rabbits.*

§ 57. The brain of the rabbit being devoid of convolutions, it is more difficult to define the exact points of stimulation. The position of the various centres was fixed in the accompanying figure by careful comparison with the dead brain during the process of experimentation (fig. 36).

A shallow sulcus (×) running parallel with the longitudinal fissure may be regarded as homologous with that marking off the superior external convolution in the dog and cat. The position of the fissure of Sylvius is indicated by a shallow depression between the narrow frontal and the broad posterior lobe, from the lower extremity of which the olfactory tract (o) is seen to spring.

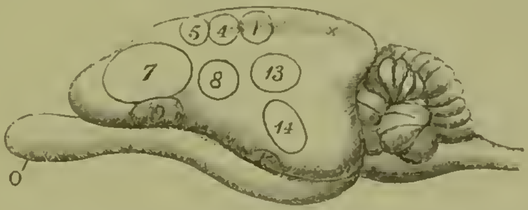


FIG. 36.—Left Hemisphere of the Brain of Rabbit. o. The olfactory bulb. × . Parallel sulcus. The signification of the circles and numerals is given in the text.

(1) A point which is situated at the anterior extremity of the shallow sulcus, parallel to the longitudinal fissure.

Advance of the opposite hind leg from an extended position.

(4) *Retraction with adduction of the opposite fore-limb.*

(5) *Elevation of the shoulder and extension forward of the fore-limb*, as in the act of stepping forwards.

(7) Covering a large extent of the frontal aspect of the hemisphere.

Retraction and elevation of the angle of the mouth, with frequently repeated chumping or munching action of the jaws, while the head becomes gradually turned to the opposite side.

(8) Just posterior to the above-mentioned.

Closure of the opposite eye, combined with elevation of the cheek and angle of the mouth, and occasionally with some undefined movement of the ear.

(9) On the orbital aspect of the frontal region.

Opening of the mouth, with movements of the tongue.

(†) I have not been able to differentiate any centres corresponding to (11) and (12), in the monkey or dog.

(13) On the parietal region.

Generally a *forward movement of the opposite eye*, and occasionally *turning of the head to the opposite side.*

In one or two instances the pupil appeared to contract, though this was regarded as doubtful.

(14) *Sudden retraction and elevation or pricking up of the opposite ear*—this occasionally coinciding with a sudden start, apparently as if the animal were about to bound forward.

(15) *Torsion or closure of the nostril*, generally on both sides.

Occasionally this was associated with the movement of the ear described under (14), doubtless from conjoint stimulation of the two centres.

Stimulation of other parts of the brain gave no definite results, though in one case, on slipping the electrodes just within the longitudinal fissure posteriorly, a sudden spasmodic extension of the opposite hind leg and general shudder were produced.

Experiments on Guinea Pigs.

§ 58. The brain of the guinea-pig (fig. 37) is almost an exact copy of that of the rabbit. The results of electrisation are essentially the same.

FIG. 37.—Left Hemisphere of the Brain of the Guinea-pig. O. The olfactory bulb. The signification of the circles and numerals is given in the text.

The numerals have the same signification as those on the brain of the rabbit.

(1) *Advance of the hind leg.*

(5) *The fore-paw is lifted* as if to step forward, and then rapidly withdrawn and adducted. The two movements of (4) and (5) in the rabbit could not be separately differentiated.

(7) As in the rabbit, *retraction and elevation of the angle of the mouth*, grinding movements of the jaws, and ultimately dragging of the head to the opposite side.

(8) *Closure of the eye and elevation of the cheek.*

(9) *Mouth opened.*

(14) *Pricking of the opposite ear.*

Experiments on Rats.

§ 59. Several experiments were made on albino rats. The results obtained were essentially the same as those in guinea-pigs and rabbits. The centres for the movements of the limbs, however, are situated nearer the frontal extremity of the hemisphere than in rabbits and guinea-pigs. The accompanying figures (figs. 38, 39) indicate by the same numerals the centres corresponding to those of the rabbit and guinea-pig, a separate individual description being unnecessary.

FIG. 38.—Upper Surface of the Brain of the Rat. o. The olfactory bulb.

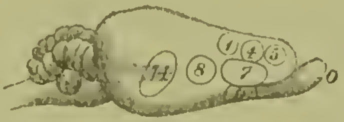


FIG. 39.—Right Hemisphere of the Brain of the Rat. o. The olfactory bulb. The signification of the circles and numerals is given in the text.

SECTION V.—*Experiments on Pigeons.*

§ 60. The brain of the pigeon (fig. 40), as well as of the common fowl, on which I have also made experiments, though apparently constructed on the same type as the brain of rodents, differs from these in the fact that electrical irritation fails to excite analogous movements. In my first experiments I had observed no result whatever on irritation of the hemisphere in any part; but in subsequent experiments, I found I had missed a very definite and constant reaction, observable in connection with stimulation of a region marked on the accompanying figure (fig. 40 ×). Irritation of this point, which is situated in the upper parietal region, causes intense contraction of the opposite pupil, occasionally associated with turning of the head to the opposite side.

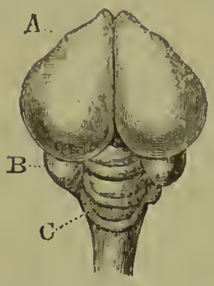


FIG. 40.—Brain of the Pigeon.

In a few cases I have also observed, from stimulation of the region below this, turning of the head to the opposite side without contraction of the pupil. Beyond these effects, the results of stimulation were entirely negative.

Experiments on Frogs.

§ 61. Experimentation on the brain of the frog with the electrical stimulus, for purposes of localisation, is scarcely possible, owing to the small size (fig. 41), and the consequent danger of conduction to adjacent structures.

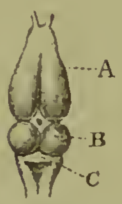


FIG. 41.—Brain of the Frog. (Enlarged × 2.)

On irritation with very fine blunted needle electrodes, closely approximated, I have observed movements of the opposite limbs on stimulation of one hemisphere; but beyond the mere fact of cross-action, nothing more could be accurately determined.

Experiments on Fishes.

§ 62. Similar difficulties are encountered in the exploration of the hemispheres in fishes. Exposure of the brain and fixation of the animal for purposes of experiment are, however, comparatively easy. The method I adopted was to secure the body in a clamp, fixed in a stand so placed as to keep the mouth of the fish under water in a trough kept at the same level by a constant stream. Free play was allowed to the tail and fins. Irritation of the hemisphere caused the tail to be struck to the opposite side, and the pectoral, anal and dorsal fins to be

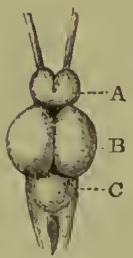


FIG. 42.—Brain of the Carp.

thrown into action, but the movements were too complex and irregular to admit of exact description.

Along with these movements the eyes were generally moved forwards or inwards.

SECTION VI.—ELECTRICAL STIMULATION OF THE BASAL GANGLIA.

Corpora Striata (*Fig.* 5, 2).

§ 63. The results of stimulation of the corpora striata in monkeys, cats, dogs, jackals and rabbits are so uniform as to admit of being generalised together.

Irritation of the corpus striatum causes general muscular contraction on the opposite side of the body. The head and body are strongly flexed to the opposite side, so that the head and tail become approximated, the facial muscles being in a state of tonic contraction, and the limbs maintained in a flexed condition. Apparently the individual movements excited from the various regions of the hemisphere are all thrown into action simultaneously, the flexors predominating over the extensor muscles.

In the case of the rabbit the pleurosthotonus is not so complete, nor is tonic spasm maintained during stimulation, for the alternate grinding movements of the jaws continue.

Individual or differentiated movements are not capable of being excited by application of the electrodes directly to the corpus striatum. Carville and Duret have arrived at the same conclusion. In Dr. Burdon Sanderson's experiments, the occurrence of individual movements, after removal of the cortical substance, is due to stimulation of the medullary fibres connecting the cortical centres with corresponding centres in the corpus striatum, which, however, are not capable of individual excitation when the electrodes are directly applied to the ganglion itself.

In the corpus striatum there would thus appear to be an integration of the various centres which are differentiated in the cortex.

Optic Thalami (*Fig.* 5, 3).

In monkeys, cats, dogs, and jackals I have not observed any outward manifestation on irritation with a current sufficient to excite active muscular contraction, when applied to the corpus striatum at the same time. The only exception (and it may have been accidental) I have noted was that, in a monkey, the application of the electrodes to the internal surface of the optic thalamus, in the region of the soft commissure, caused a spasmodic extension of the legs.

In rabbits also the effect in general was entirely negative, with one exception. In this the application of the electrodes to the optic thalamus caused movements of the eyes, twitching of the opposite ear, shuddering and spasmodic movements of the limbs and general restlessness,—phenomena which might be regarded as indications of general irritation of sensory centres.

CHAPTER IX.

THE HEMISPHERES CONSIDERED PHYSIOLOGICALLY.

§ 64. In the preceding chapter only a bare description has been given of the phenomena of electrical irritation of the cerebral hemispheres in various classes of animals, classified in such a manner as to allow of comparison with each other. It will be seen that, notwithstanding certain individual differences, there are many striking resemblances, which may be made the basis of anatomical and physiological homologies.

Though many of the movements described have evidently a purposive or volitional character, the signification of others is more obscure, and it has still to be determined what is the real relation between excitation of a given part of the cortex and the resulting motor manifestations. The mere fact of motion following stimulation of a given area does not necessarily signify a motor region. The movements may be the result of some conscious modification incapable of being expressed in physiological terms, or they may be reflex, or they may be truly motor in the sense of being caused by excitation of a region in direct connection with the motor parts of the crus cerebri.

The method of stimulation by itself is incompetent to decide these questions, and requires to be supplemented by localised destruction of those areas, stimulation of which is followed by definite motor manifestations.

In my endeavours to arrive at the physiological significance of the facts recorded in the preceding chapter, I have made experiments chiefly on the brain of monkeys. The brain of these animals is constructed on the same type as the human brain, and their habits are such as to afford the most reliable data for inferences applicable to the physiology of the brain of man. This is more especially the case in reference to the existence or not of sensation, as it is often extremely difficult to distinguish between conscious and reflex reaction to sensory stimuli.

The localised destruction of special areas was effected principally by means of the actual cautery, varied occasionally with excision of the part. The observation of the effects and the application of various tests were supplemented by careful *post-mortem* examination of the extent of the lesion and the general condition of the brain.

The fuller details of this series of experiments are recorded in the 'Philosophical Transactions,' Vol. II., 1875, to which reference is made.

Section I.—Sensory Centres.

The Angular Gyrus (*Pli Courbe*).

§ 65. In the preceding chapter, the results of stimulation of this convolution have been recorded under (13) and (13′), (fig. 29). The effects in general are movements of the eyeballs, frequently associated with movements of the head to the opposite side, and very often contraction of the pupils.

The corresponding region in the brain of the cat, dog and jackal is the parietal aspect of the second external convolution. (Figs. 32, 33, 35.)

In the brain of the rabbit (Fig. 36) the corresponding centre likewise occupies the parietal region; and in the brain of the pigeon the centre for contraction of the pupil also occupies a similar position. (Fig. 40.)

These phenomena seem to be merely reflex movements consequent on the excitation of subjective visual sensation. Destruction of the angular gyrus on one side causes blindness in the opposite eye. The loss of vision is complete, but is not permanent if the angular gyrus of the opposite hemisphere remains intact; compensation rapidly taking place, so that vision is again possible with either eye as before. On destruction of the angular gyrus in both hemispheres, however, the loss of vision is complete and permanent, so long, at least, as it is possible to maintain the animal under observation.

When the lesion is accurately circumscribed in the angular gyrus the loss of vision is the only effect observable, all the other senses and the powers of voluntary motion remaining unaffected.

In support of these conclusions, the following details selected from the protocols of the several experiments recorded elsewhere, will be sufficient. In the first experiment the angular gyrus of the left hemisphere was destroyed, the left eye was securely bandaged, and the animal allowed to recover from the state of chloroform narcosis. After recovery it began to grope about a little *in loco* perfectly alert, but would not move from its position. It did not flinch when held close to the gas-light. Placed in the cage beside its companions, it took no notice of them, but sat still. Hearing and other senses remained unaffected, and stimuli of these senses caused active reaction.

After it had remained in this condition for an hour without alteration, the bandage was removed from the left eye. When placed on the floor it immediately looked round, and ran nimbly to the cage and joined its companions. When again held up to the light as before, it flinched and turned away its head. The change in the animal's manner after removal of the bandage was of the most striking character. Next day, however, on the left eye being again bandaged, the animal gave evidence of sight by running up to its cage, the door of which was shut, and lapping water from a dish, which it reached by inserting its hand between the bars.

In a second case, in which the angular gyrus was destroyed in one hemisphere, the results were almost precisely of the same nature; the removal of the bandage from the eye on the same side being followed by an instantaneous change in the animal's behaviour, indicating the sudden transition from a state of blindness to restoration of sight.

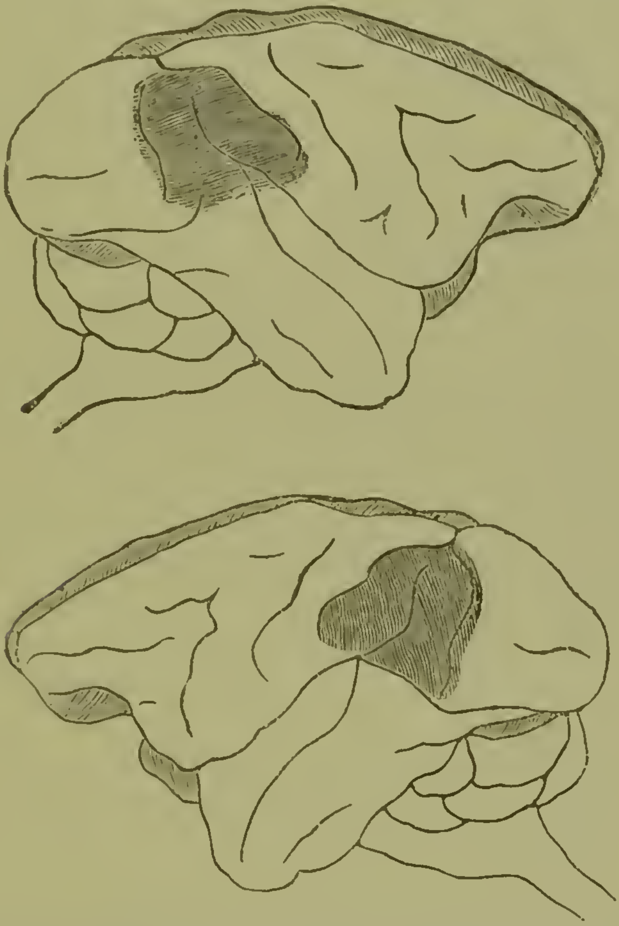
In another experiment the angular gyrus was exposed on both sides, and accurately cauterised. For a long time I could devise no test of sight which should be free from the fallacy attending mere reflex reaction to visual impressions. For the animal sat still and refused to stir from its place, so that there was no means of determining whether it could walk steadily and avoid obstacles in its path. The pupils contracted to light, and light flashed in the eyes caused the animal to wince. When a piece of apple was dropped near it, so as just to come in contact with its hand, it took it up, smelt it, and ate it with gusto. When called to, it would turn and look in the direction of the sound. With the exception of the reluctance to move from its position, arising evidently from a sense of insecurity, there was nothing to indicate decisively whether the animal was really blind. I had found before the experiment was performed, that this animal was exceedingly fond of tea, and would run anywhere after it. On placing a cup of tea close to its lips it began to drink eagerly. The cup was then removed from immediate contact, and the animal, though intensely eager to drink further, as indicated by its gestures, was unable to find the cup, though its eyes were looking straight towards it. This test was repeated several times with exactly the same result. At last, on the cup being placed to its lips, it plunged in its head and continued to drink, though the cup was gradually lowered and drawn half-way across the room.

The animal retained complete muscular power, and every other form of sensation except sight; the condition as regards which being repeatedly tested in various ways.

On *post-mortem* examination next day, the angular gyri were found completely disorganised, the rest of the brain being of normal appearance (figs. 43, 44).

The results of several other similar experiments were such as to confirm those given, and the conclusions above stated.

Certain very important physiological questions are decided by these facts of experiment. They show that the destruction of the angular gyrus causes no motor paralysis. Hence the movements consequent on electrical stimulation are to be regarded merely as reflex indications of sensory stimulation. Whether these movements are due to the associated action of motor centres in the hemispheres, or to the associated action of lower centres, cannot be determined experimentally. As to the complete cross action of the hemispheres in reference to vision, these experiments return a very decided answer. The destruction of one angular gyrus does not cause hemiopia or partial blindness in both eyes, but complete blindness in the opposite eye only. Had only one half of the retina been paralysed in the monkeys in which the angular gyrus on one side was destroyed, vision would still have remained sufficient at least to enable the animal to direct its movements, though with less precision than before. This, however, was not the case, for the sudden change after the removal of the bandage from the eye on the same side as the lesion, indicated, not better vision, but a sudden transition from complete blindness to restoration of sight.



FIGS. 43 AND 44.—The shaded portions in these figures indicate the lesions of the cortex of the hemispheres in the monkey, causing blindness. (Roy. Soc.)

These facts would seem to bear out the recent investigations of Biesiadecki and others, which appear to show that there is total decussation of the optic nerves in the optic chiasma in the monkey and man, as in the lower animals, a view which is also supported by Dr. Bastian ('Paralysis from Brain Disease,' p. 114).

But Charcot ('Le Progrès Medical,' Aug. 1875) has recently propounded an ingenious scheme of the construction of the optic chiasma, which is at once in harmony with the fact that lesions of the chiasma cause hemiopia, while lesions of the visual centre in the hemisphere produce complete unilateral blindness in the opposite eye.

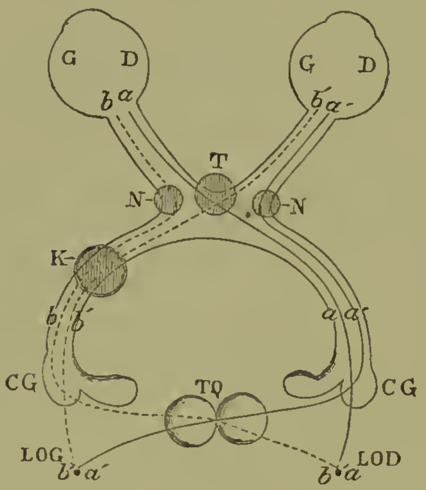


FIG. 45.—Scheme of the Decussation of the Optic Tracts, according to Charcot. T. Semi-decussation in the optic chiasma. TQ. Decussation posterior to the corpora geniculata. CG. Corpora geniculata. *a′ b*. Fibres which do not decussate in the chiasma. *b′a*. Fibres which undergo decussation in the chiasma. *b′a′*. Fibres coming from the right eye which meet in the left hemisphere LOG. LOD. Right hemisphere. K. Lesion of the left optic tract, producing right lateral hemiopia. LOG. A lesion at this point, producing right amblyopia. T. Lesion producing temporal hemiopia. NN. Lesion producing nasal hemiopia.

Among the fibres of the chiasma are some (*b′ a*) which cross to the opposite eye, and others (*a′ b*) which pass to the eye of the same side. The latter lie externally, while the former occupy a more central position in the optic tracts. Each tract in fact contains fibres for each eye, the external for the eye on the same side, the internal for the corresponding half of the opposite eye. Hence, lesion of the left side of the chiasma, or of the left optic tract (K), will cause hemiopia of both eyes, paralysing the left side of both retinæ.

The external fibres, or those which do not decussate in the chiasma, decussate with their fellows in the corpora quadrigemina (TQ), and so reach the opposite hemisphere; while the fibres which decussate in the chiasma do not again decussate in these ganglia, but pass directly through the corpora geniculata (CG) into the hemisphere (LOG, LOD). In consequence of this arrangement, all the fibres of the right eye reach the left hemisphere, and all those of the left eye the right hemisphere.

Hence, lesion of the cerebral centre causes complete blindness of the opposite eye; while lesions lower down, whether in the corpora quadrigemina, corpora geniculata, or optic tracts affecting the two sets of fibres before they have run their complete course, cause partial blindness, or hemiopia of each eye. (See fig. 46, with description.)

This scheme, though not demonstrated anatomically, serves to explain satisfactorily many of the facts of clinical observation.

Another fact of great importance brought out by these experiments, is that sight with both eyes is still possible after complete destruction of the visual centre on one side. A process of compensation takes place if the visual centre in one hemisphere remains intact. Whether this is complete cannot be determined in the lower animals, but it is evidently sufficient for their ordinary modes of activity. That the compensation depends on the integrity of the other centre, is shown by the fact that total blindness of a permanent character ensues when both centres are destroyed.

This can only be explained on the supposition that in the lower centres, the corpora quadrigemina or corpora geniculata, the nuclei of the optic tracts are so bilaterally associated as to render it possible for both to maintain such relations with either hemisphere as to furnish the conditions of visual perception with both eyes after complete destruction of the visual centre in the one hemisphere. The existence of such a compensatory relation between the two hemispheres, will account for the comparative rarity of blindness from unilateral lesions of the grey matter of the hemispheres in man. Here of course we exclude blindness resulting from secondary degeneration of the optic nerves or retinæ, as in cerebral tumours. As degenerations of the grey matter are usually of slow growth, and as reciprocal compensation is comparatively rapid, the absence of complete blindness in one eye, even though the visual centre in the opposite hemisphere be completely degenerated, presents no difficulty when viewed in the light of the foregoing experiments. A sudden organic or functional suspension of the action of the visual centre should, however, be expected to manifest itself in temporary unilateral blindness or disturbance of vision. It not unfrequently happens that sight is lost or impaired on the same side as motor paralysis from brain disease. This, according to Dr. Bastian (*op. cit.* p. 113), is more particularly the case when embolism occurs in the posterior cerebral artery. He accounts for the affection of sight by supposing that the optic tract, or the corresponding pair of corpora quadrigemina, are affected by the lesion.

It appears to me, however, that sudden functional disturbance of the cerebral visual centre may equally well account for the symptoms.

The phenomena of cerebral hemianæsthesia, to be afterwards discussed, are quite in accordance with the localisation of the visual centre in the region specified, and with the experimental evidence of its cross action. In this case, however, the lesion causing (with other symptoms) loss or impairment of vision in the opposite eye, is situated not in the visual centre itself, but in the medullary fibres, which connect it with the optic nuclei and ganglia.

As regards the effects of destruction of the homologous regions of the brain in the lower animals, there are fewer exact experimental data. Flourens found that removal of the cerebral hemisphere on one side as a whole, abolished sight in the opposite eye, but he did not attribute this to lesion of any particular part. The following experiment on a cat shows that blindness results from lesion of a region which the effects of electrical irritation indicate to be homologous with the visual centre in the monkey. The grey matter of the left hemisphere was destroyed by the cautery in the region marked (13) in fig. 35; the lesion extending slightly on each side into the superior and third external convolutions.

The left eye having been securely closed, the animal was allowed to recover from the effects of chloroform. On recovering it began to grope about, keeping its right eye open, and after a short interval began to walk about the room, but constantly knocking its head against obstacles. After two hours the left eye was unclosed. The animal now walked with greater freedom, and avoided obstacles generally, but occasionally it ran against them, a circumstance which I think was attributable to the blindness still existing in the right eye.

This experiment confirms those on monkeys, and indicates the homologous region in the brain of the cat.

The experiments of Dr. McKendrick on pigeons ('Observations and Experiments on the Corpora Striata and Cerebral Hemispheres of Pigeons,' presented to the Royal Society of Edinburgh, January 1873, Reprint, pp. 32) show that destruction of the region marked × on fig. 40 causes blindness in the opposite eye.

He found that removal of the anterior part of the hemisphere had no effect on vision, nor removal of the posterior part of the hemisphere. When, however, that part of the brain was removed which corresponds with the situation of fig. 40, vision was destroyed on the opposite side. Dr. McKendrick is careful to distinguish between consciousness of, and mere reflex response to, retinal impressions; and comes to the conclusion that visual sensation or consciousness of visual impressions is abolished by the lesion in question.

Further experiments on the lower animals, with the view of determining homologous regions, would be very desirable.

The Superior Temporo-Sphenoidal Convolution.

§ 66. Irritation of this convolution fig. 29 (14), in the monkey is followed by certain definite results, *viz.*, sudden retraction or pricking up of the opposite ear, wide opening of the eyes, dilatation of the pupils, and turning the head and eyes to the opposite side.

These phenomena resemble the sudden start and look of astonishment or surprise which are caused when a loud sound is made in the ear opposite the hemisphere which is being irritated. This is illustrated by the following simple experiment. A monkey was placed on a table, and while all was still and quiet a shrill whistle was made close to the animal's right ear. Immediately the ear was pricked, and the animal turned with an air of intense surprise, with eyes widely opened and pupils dilated, to the direction from which the sound proceeded. On repetition of the experiment several times, though the pricking of the ear and the turning of the head and eyes in the direction of the sound constantly occurred, the look of surprise and dilatation of the pupils ceased to be manifested.

From the mere character of the reactions, without further experimental demonstration, it might fairly be concluded that the movements are the outward manifestations of the arousal of subjective auditory sensation, and that we have in the temporo-sphenoidal convolution not a motor centre, but a centre of auditory sensation, stimulation of which causes in a reflex manner the movements in question. It is not, in my opinion, possible to determine experimentally whether in this case the movements are called forth through the agency of the lower centres only, or whether they are dependent on the associated action of a special centre in the motor region of the brain. The latter hypothesis seems the more probable, for the phenomena of irritation of this convolution are, with the important exception of the pricking of the ear, identical with those consequent on stimulation of (12), in the frontal region of the hemisphere. It would seem, therefore, that the pricking of the opposite ear is the special reflex indication of subjective auditory sensation, and that the other reactions are indications of the associated activity of a centre specially concerned in the movements characteristic of attention, or, if strongly excited, of astonishment or surprise.

Still more characteristic, perhaps, are the effects observed on stimulation of the homologous regions of the brain in some of the lower animals, whose habits are such as make their safety depend on the acuteness of their hearing. In the cat, dog and jackal, the posterior division of the third external convolution marked (14) in the various figures 32, 33, 35, is the physiological homologue of the superior temporo-sphenoidal convolution of the monkey.

In the brain of the rabbit, a region corresponding with this in situation (fig. 36, 14) gives similar results on stimulation, *viz.*, pricking of the opposite ear, frequently associated with turning of the head and eyes to the opposite side. But in the wild jackal and the timid rabbit stimulation of this part caused not only reflex pricking of the ear, but the quick start or bound as if to escape from danger, such as might be indicated by loud or unusual sounds.

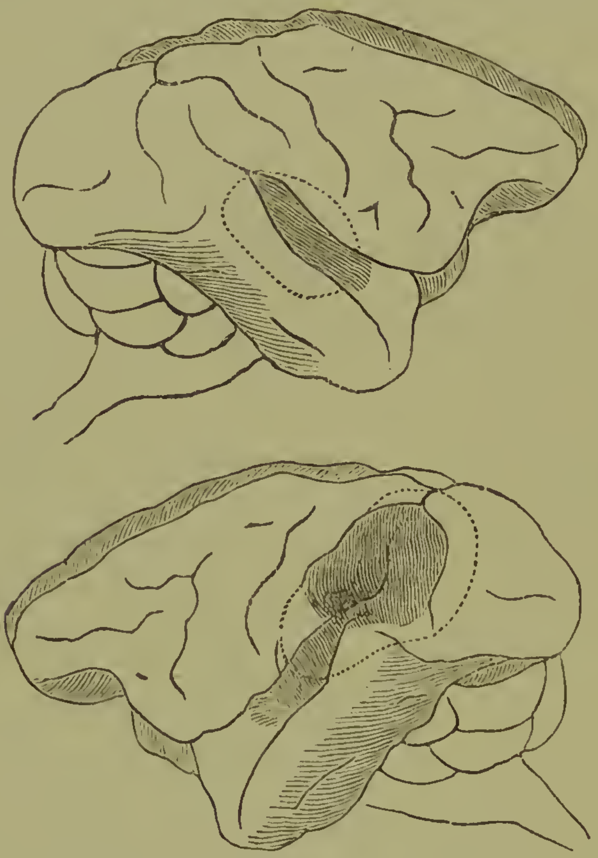
In the pigeon the absence of the auricle renders it difficult to fix on any simple movement as the reflex expression of auditory sensation; but the occasional turning of the head to the opposite side, on stimulation of the parietal region below and posterior to the visual centre, may perhaps be significant of essentially the same fact. In addition to the strong presumption furnished by the character of the reactions, that the superior temporo-sphenoidal convolution (or its homologue in the brain of the lower animals) is the centre of hearing, the results of localised destruction of this convolution are such as to indicate annihilation of the sense of hearing, and of this only.

To test the sense of hearing in the lower animals, and to distinguish between merely reflex reaction to auditory impressions and true auditory sensation, is perhaps a more difficult problem, than to make such differentiation in respect of the other senses. There is, further, the greater difficulty of determining the existence or absence of unilateral deafness, on account of the impossibility of absolutely restricting a sonorous vibration to one side alone. By plugging the sound ear this may in a great measure be overcome; but the possibility of the communication of sonorous vibrations through the skull apart from the tympanic apparatus must always be taken into account.

In many of the experiments which I made on the temporo-sphenoidal lobe, the lesion was not limited to the superior temporo-sphenoidal convolution, and hence the special effects could only be reached by a process of exclusion. Without describing in detail the individual experiments, I will only give the general results. When the temporo-sphenoidal convolutions were destroyed, with careful avoidance of the angular gyrus, the animal continued to see as before, and to retain all its powers of voluntary motion. When the lesion was confined to one side, and involved the superior temporo-sphenoidal convolution, the animal continued to respond to auditory stimuli, turning its head if called to—reactions, however, which did not ensue when the ear on the same side as the lesion was securely stopped with cotton wool. A very loud sound made close to the ear, however, still caused a slight start, and elevation of the eyebrows. Sounds made by concussion on the floor also caused the animal to start; but in this case tactile thrill enters as a complication, and the reaction cannot be regarded as of a purely auditory nature.

When the lesion was established bilaterally, so as to cause destruction of the superior temporo-sphenoidal convolution on both sides, along with certain other effects not depending on localised injury to this convolution, the animal, though fully conscious and on the alert to everything attracting sight, failed to respond to auditory stimuli usually exciting active reaction and attention.

The following experiment was made with the view of limiting the lesion to the superior temporo-sphenoidal convolution on both sides, so as to avoid the complications induced by more extensive destruction of the temporo-sphenoidal lobe. The angular gyrus had just been cauterised on the left side, with the effect of causing blindness in the right eye alone, and without any affection of hearing or the other senses. The superior temporo-sphenoidal convolution was then exposed and cauterised on both sides; the lesion, as was ascertained *post mortem*, being confined to this region (figs. 46, 47). After complete recovery from the operation, the various senses and powers of voluntary motion were tested repeatedly. Touch, taste and smell were



Figs. 46 and 47.—The shading in these figures indicates the position of the lesions of the cortex in the hemispheres of the monkey, causing loss of hearing in both ears, and loss of sight in the right eye. The dotted line indicates the extent of the surface exposed by removal of the skull. (Roy. Soc.)

perfect, and sight, as indicated by the animal's perfect freedom of movement and ability to find its food and drink, practically unimpaired twenty-four hours after the operation. As regards hearing, it was difficult to devise a satisfactory test, owing to the alertness of the animal, and the attention it gave to everything around it. A loud sound made close beside it caused a start, which, however, could not be taken as a proof of hearing proper as distinguished from reflex reaction.

In order to avoid attracting its attention by sight, I retired behind the door and watched the animal through a chink, while it sat comfortably before the fire. When all was still I called loudly, whistled, knocked, &c., without attracting the animal's attention to the source of the sound, though it was sitting perfectly awake and looking around. On my cautiously approaching it, it remained unaware of my proximity until I came within the field of vision, when it started suddenly and made grimaces as if in terror or alarm. On repeating these tests when the monkey was sitting quietly along with a companion monkey whose powers of hearing were unquestionable, the companion invariably became startled at the sounds, and came peering curiously to ascertain their origin, while the other remained quite still.

Ten hours subsequently I again repeated these various tests with the same results—results which justified the conclusion that whether the animal heard or not, it certainly gave no signs of hearing that which, in another animal, excited lively curiosity. Beyond this, without personal testimony from the subject of experiment, it is impossible to go, but I think that when the two sets of experiments are taken together,—*viz.*, the positive reactions to electric stimulation, and the absence of reaction to usual forms of auditory stimuli when the superior temporo-sphenoidal convolutions were destroyed,—the evidence of the localisation of the centre of hearing in this region amounts to positive demonstration.

Such reactions as result from loud sounds made in close proximity to the organ of hearing, are to be regarded as only reflex phenomena, of the same nature as those observed by Flourens, in the case of pigeons deprived of their hemispheres, when a pistol was fired close to the head.

The Hippocampal Region.

§ 67. The term hippocampal region is employed here to signify the hippocampus major and uncinate convolution, it being impossible to separate them from each other experimentally. A lesion sufficient to destroy the uncinate convolution necessarily involves the subjacent hippocampus major, and the destruction of the hippocampus major cannot be effected without injury to the medullary connections of the uncinate gyrus. For these reasons, I do not attempt to differentiate between lesions of the hippocampus major and lesions of the uncinate convolution, but class the two under the head of lesions of the hippocampal region generally.

Owing to the internal position of this part of the brain, it is impossible to reach it for purposes of isolated stimulation with the electrodes, without such operative procedure as would vitiate the experiment. Destructive lesions of this region abolish tactile sensation on the opposite side of the body, as will be shown by the experiments described below. It might, therefore, be expected that irritation of this region should cause outward manifestations of the arousal of subjective sensation, similar, *cæteris paribus*, to those excited by irritation of the centres of sight and hearing. I have already, in the preceding chapter, called attention to certain phenomena which, owing to unavoidable sources of error, were regarded as of doubtful import, but which are capable of being interpreted in accordance with this view.

In one case, on irritation of the inner and lower aspect of the occipital lobe in a monkey, at a point which would correspond to the upper end of the uncinate convolution, the animal exhibited signs of restlessness and uneasiness, turning its head to the opposite side and backwards, as if conscious of some uncomfortable tactile sensation, chiefly in the opposite limbs. In the cat, dog and jackal, similar phenomena were occasionally seen to occur when the electrodes were applied to the recurved posterior extremity of the hemisphere, especially when the position of the electrodes and the strength of the current were such as might cause irritation of the hippocampal region.

A similar result was recorded in the case of a rabbit, when the electrodes were applied to the inner and posterior aspect of the hemisphere.

Owing to the uncertainty as regards the localisation of the irritant, doubts may be entertained as to the correctness of the view which I am inclined to adopt, *viz.*, that the phenomena were consequent on irritation of the centre of tactile sensation; but the fact of their occurrence, almost identically, in so many different animals, from irritation of what anatomically may be regarded as homologous regions, favours the supposition.

More reliance, however, is to be placed on the result of destructive lesions for the exact localisation of the region of tactile sensation.

After numerous experiments, in which almost the whole outer surface of the hemisphere had been successively destroyed without causing loss of the sense of touch, it seemed to me strange if such an important intellectual sense should not, like the others, have a special centre in the hemisphere. My attention was, therefore, directed to the inner aspect of the temporo-sphenoidal lobe, and to devise a method by which this region might be reached and destroyed.

In various experiments with the view of determining the centres of hearing, and the centres of smell and taste, deep-seated lesions were established in the temporo-sphenoidal lobe, sometimes in one hemisphere, sometimes in both. In several cases, the details of which are recorded elsewhere, tactile sensibility was impaired, or absolutely destroyed, when the destructive lesion had involved the hippocampal region. This was shown by the absence of reaction to cutaneous stimulation, and, perhaps, more conclusively, by the fact that the animal ceased to employ the limbs of the affected side for purposes of touch or prehension, though the symptoms of true motor paralysis were absent.

As the examination of the brain in all these cases where tactile sensation was impaired or abolished, revealed lesion or complete destruction of the hippocampal convolution, I endeavoured to destroy this region directly, without causing lesion of the convolutions on the external surface. This, at first sight seemed impossible, but ultimately I hit upon a method by which the complication of affection of the other senses at least might be avoided.

The plan I adopted was to reach the internal aspect of the temporo-sphenoidal lobe from the occipital region. I had previously determined by various experiments that destruction of the occipital lobe caused no affection, either of special sense or of the powers of voluntary motion, and hence such lesions as might be caused in this lobe in the attempts to reach the hippocampal region would not interfere with the positive results which might ensue. By repeated trials on the dead brain, I succeeded in ascertaining the direction in which a wire might be made to penetrate the tip of the occipital lobe, and traverse the hippocampal convolution throughout its whole extent. With the wire cautery I then made several attempts in the narcotised animal with varying degrees of success, as determined by *post-mortem* examination. In the following case it was found that the cautery had ploughed a channel through, and disorganised the hippocampal convolution and uncinate gyrus, without injury to the convolutions on the external surface, or affection of the basal ganglia, crura cerebri, or cerebral nerves, as was ascertained by post-mortem examination before secondary inflammatory changes were set up (see fig. 48). The conditions of experiment were, therefore, such as to warrant the strict relationship of cause and effect between localised destruction of the hippocampal region and the observed symptoms.

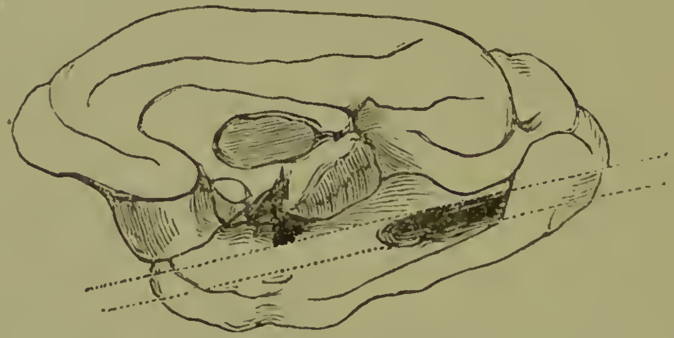


FIG. 48.—The Internal Aspect of the Right Hemisphere of the Brain of the Monkey. The shading and dotted lines indicate the track of the cautery and position of the lesion, causing loss of tactile sensation on the left side of the body. (Roy. Soc.)

As regards the existence or absence of tactile sensation, the same kind of difficulty is encountered as in the other senses, *viz.*, the differentiation of mere reflex reaction to stimulation from conscious perception. As Flourens remarks, ‘On sent combien il est difficile de discerner le cas où il *touche* du cas où il est simplement touché.’

Appreciating this difficulty, I therefore endeavoured to apply such tests as might clearly distinguish between the two cases, relying more on the evidence furnished by the spontaneous activity of the animal than on mere response to cutaneous stimulation.

The monkey in question, which was the subject of the present experiment, was found to be, as a rule, left-handed, taking things offered to it preferably with the left hand. For this reason the right hippocampal region was destroyed, with the view of affecting the sense of touch in the limb which the animal usually employed.

After recovery from the operation and the narcotic stupor, sight and hearing were found to be unimpaired, and the intelligence quick and active as before. But cutaneous stimulation by pricking, pinching, or pungent heat sufficient to cause lively manifestations of sensation when applied to the right side of the body, failed in general to elicit any reaction whatever on the left side, whether face, hand, or foot. Only occasionally, when the stimulus was intense or long-continued, did reaction at all ensue. This most remarkable absence of response of any kind rendered the fact of annihilation of tactile sensibility almost completely proved without further evidence. But the abolition of tactile sensation was further conclusively shown by the condition as to motility of the left limbs. There was no flaccidity of the muscles, and no facial distortion as is observed in motor hemiplegia, but the arm was kept motionless by the side, and the leg straddled outwards, or was placed irregularly, and yet a certain amount of voluntary control was retained over the limbs. This was exemplified by the following incident which occurred in the course of the observations:—

On being placed within its cage, the animal mounted its perch, gaining its position with some difficulty on account of its tendency to fall over on the left side. While endeavouring to turn on its perch the left foot slipped off, whereupon, in the struggle to recover its equilibrium, the animal clutched with both hands at the bars of the cage, but grasped only with the right hand, the left being powerless. Aided by its teeth and right hand it recovered its position, and after grasping the perch firmly with its right foot, ultimately dragged up the left leg. This position of steadiness, however, was possible only while the animal kept on the alert. On its dropping off to sleep, which it continually tended to do, the left foot would slip off, and again the same struggle would occur to regain equilibrium. In all these occurrences, though movements of the left limbs were sometimes made, no prehensile or other independent action of the left hand or leg was ever manifested. The animal scratched the right side of its body, which seemed to itch considerably, with its right hand, and used its right hand for prehension, instead of the left, as before. The paralysis of motion in this case was not true motor paralysis, which, as will be afterwards shown, results from lesion of a totally different part of the brain, but the paralysis of motion which is due to the loss of tactile sensation, by which movements are guided.

§ 68. The experiments of Bell, Majendie and others on the sensory branches of the fifth nerve, showed that a condition of paralysis of the facial muscles resulted, so closely resembling motor paralysis, as to cause mistake as to the true function of the nerves in question. Several remarkable cases are on record illustrative of the effects of loss of tactile sensation on movement, and on the consciousness of muscular contraction. Though the first effect of paralysis of tactile sensation is to cause cessation of voluntary movements, yet the power of movement remains, and is capable of being exercised.

Without tactile sensation, however, the limb becomes practically an inanimate instrument. Its locality and the state of contraction of its muscles, are cut out of consciousness; and though it may be moved by the agency of the motor centres, it can only be used, and its movements directed, under the guidance of the eye, which enables the individual to place the limb in such positions as previous experience has associated with the accomplishment of certain desired effects. The directing agency of the eye being withdrawn, the position of the limb may be altered unconsciously, and a weight previously supported will fall to the ground, a fact of which the individual only becomes aware by other channels of perception.

Neither the contraction of the muscles induced by the agency of the motor centres, nor the most powerful contraction induced by the electric current, rise into consciousness. This condition is well seen in cerebral hemianæsthesia, in which tactile sensation is entirely destroyed, while the power of voluntary motion remains. Cases of this kind have been carefully recorded by Demeaux, Magnan and others.

The following remarks by Demeaux, in reference to a female patient, the subject of this affection, I quote in the original, as a graphic description of the condition caused by loss of tactile sensation:—'Elle mettait ses muscles en mouvement par l'influence de sa volonté, mais elle n'avait pas conscience des mouvements qu'elle exécutait; elle ne savait pas dans quelle position était son bras; il lui était impossible de dire s'il était étendu ou fléchi. Si l'on engageait la malade à porter la main à son oreille, elle exécutait immédiatement le mouvement; mais si ma main venait s'interposer entre la sienne et l'oreille, elle n'en avait pas conscience; si j'arrêtais son bras au milieu du mouvement, elle ne s'en apercevait pas. Si je fixais, sans la prévenir, son bras sur son lit et lui disais de porter la main à sa tête, elle luttait un instant, puis cessait d'agir, croyant avoir exécuté le mouvement. Si je l'engageais à recommencer, lui montrant que son bras était resté à la même place, elle luttait avec plus d'énergie, et dès qu'elle était obligée de mettre en jeu les muscles du côté opposé, elle reconnassait qu'on mettait obstacle au mouvement.' (Thèse, 'Des Hernies Crurales,' which contains, p. 96 *et seq.*, an account of a case of Hemianæsthesia. Paris, 1843, p. 100.) These facts militate strongly against the existence of a muscular sense independent of the centres and paths of centripetal impressions from the skin, muscles, fasciæ, joints and ligaments, all of which, as we have already seen (p. 51), enter into the composition of this so-called sense. (Further, *vide* § 75.)

Unlike the effects of destruction of the angular gyrus, those resulting from destruction of the hippocampal region are, as far as observation could be maintained, of a persistent character.

Valuable corroboration of the fact of localisation of the true centre of tactile sensation in the cortex cerebri, as distinct from the pons or lower ganglia, is furnished by clinical and pathological investigation in man, though the special centre of tactile sensation has hitherto never, as far as I am aware, been reached by this method of inquiry. The investigations in particular of Charcot ('Le Progrès Médical,' Aug. 1875), Raymond (*Idem*, July 1875, 'Hémianesthésie de Cause Cérébrale'), Veyssière ('Recherches Cliniques et Expérimentales sur l'Hémianesthésie de Cause Cérébrale,' Thèse, Paris, 1874), and Rendu ('Des Anesthésies Spontanées,' Thèse, Paris, 1875), have demonstrated that rupture or disorganisation of that part of the internal capsule or peduncular expansion of the crus cerebri which lies external to the optic thalamus, causes hemianæsthesia of the opposite side of the body. Veyssière, in particular, has established the connection between division of the posterior part of the internal capsule and hemianæsthesia, both by clinical analysis and carefully conducted experiments on the lower animals, in which he ingeniously divided this set of fibres (fig. 49). Veyssière's experiments have been confirmed by Carville and Duret. In this respect both clinical and experimental investigation are quite in accord.

FIG. 49.—Vertical Transverse Section through the Brain of the Dog on a level with the Corpora mamillaria (Carville and Duret). OO. The optic thalami. SS. The nuclei caudati of the corpora striata on each side. LL. The lenticular nuclei of the corpora striata. PP. The internal capsule, or peduncular expansion. AA. The hippocampi. X. Section of the posterior part of the peduncular expansion, causing *hemianæsthesia*.

It is evident, however, that the cause of the hemianæsthesia in this case is not due to disorganisation of centres of sensation, but merely to interruption of the path of transmission from the organs of sense to the sensory centres in the cortex. The separate destination of the radiating fibres here collected together is in no wise indicated.

The experiments I have narrated clearly show that the cutaneous anæsthesia resulting from this lesion is due to interruption of the centripetal fibres which proceed to the hippocampal region. But in addition to cutaneous anæsthesia of the opposite side, there are certain other effects which afford valuable confirmation of the sensory localisation which I have established in the brain of the monkey. Vision, as a rule, is seriously impaired, if not quite abolished, on the same side as the cutaneous anæsthesia; there being a very remarkable contraction of the field of vision, and difficulty in colour discrimination. The affection of sight is absolutely confined to the one side, *i.e.*, the side opposite the cerebral lesion. There is no hemiopia, but a pure unilateral amaurosis or amblyopia. In this respect the results of experimental investigation on the monkey and clinical observation are entirely in harmony.

Veyssière in his experiments on the lower animals, has not been able to determine satisfactorily whether vision is affected by the lesion which induces cutaneous anæsthesia of the opposite side.

The symptoms caused by rupture or disorganisation of the posterior division of the peduncular expansion are identical with those described under the name of hysterical hemianæsthesia, or hemianæsthesia from alcoholism, as in a case described by Magnan ('Gazette Hebdomadaire,' Nov., 1873). Not only tactile sensibility, but all the forms of special sensibility, are affected on the side opposite the lesion. Smell is affected on the same side as the tactile sensibility, a fact which requires special consideration, as it will be shown that the olfactory centre proper is in the hemisphere of the same side.

But with the exception of the paths of olfactory sensation, section of the posterior division of the internal capsule is practically, at one blow, interruption of all the sensory tracts, and is equivalent to extirpation or disorganisation of the sensory centres of the cortex.

The differentiation of these into regions of special sense is simply a terminal specialisation of the centripetal paths which radiate from the internal capsule or foot of the corona radiata into the cortex. While we wait for confirmation, on the side of human morbid anatomy, of the localisation of special sensory convolutions—a matter, in my opinion, simply of time and care—we may regard the facts of anæsthesia of cerebral origin as the first step in this direction.

The Subiculum Cornu Ammonis and its neighbourhood.

§ 69. The experiments to be recorded in this section show that the region here indicated contains the centres both of smell and taste ; but as I have not been able accurately to determine the respective limits of these centres, they are treated of together. The anatomical connection of the olfactory tract, or rather convolution, with the tip of the temporo-sphenoidal lobe, or subiculum cornu Ammonis, so distinctly seen in the brain of the rabbit, cat, dog, etc., might of itself be regarded as establishing strong grounds for a physiological connection between this region and the sense of smell. In the monkey and in man the direct connection between the outer root of the comparatively small olfactory tract and the subiculum is not so evident, though in the monkey it is more apparent than in man. The origin of this so-called root from the subiculum, is, however, thoroughly established by microscopical investigation. The results of electrical irritation of this region are such as to confirm the view founded on anatomical considerations.

Irritation of the subiculum (15) in the monkey, cat, dog and rabbit was attended by similar phenomena in all, *viz.*, a peculiar torsion of the lip and partial closure of the nostril on the same side. This is evidently the outward expression or reflex indication of the excitation of subjective olfactory sensation of an intense character. Similar reaction is produced by the direct application to the nostril of a powerful or disagreeable odour. As a rule, the reaction was limited to the nostril on the same side, though in the rabbit both nostrils usually reacted conjointly.

The occurrence of the reaction on the same side is in harmony with the anatomical connection of the olfactory tracts, with their respective hemispheres, without decussation.

An olfactory chiasma, however, as Meynert has shown, exists in the anterior commissure. This contains fibres passing from one olfactory bulb to the other, more especially seen in the lower animals, in which the bulbs are largely developed ; and also fibres which are capable of being traced to the region of the subiculum on both sides, connecting the olfactory centres with each other.

If the anterior commissure were a decussation by which the central paths of the respective olfactory tracts were carried over to the opposite hemisphere, section of the anterior commissure would abolish smell in both nostrils. The same effect would result from complete destruction of the subiculum on one side, for not only would this lesion destroy the sensory centre for the opposite olfactory tract, but also interrupt the path of the olfactory tract on the same side in its course to the other hemisphere. It will be seen that the effect of unilateral lesion of the subiculum does not abolish smell on both sides, but causes diminution or abolition of smell on the one side, *viz.*, the side of lesion—a fact which disproves the decussation of the olfactory paths in the anterior commissure.

Neither the inner roots which fuse with the gyrus fornicatus on each side, nor the outer roots which are connected with the subicula, and thence through the posterior pillars of the fornix, with the optic thalami, undergo decussation, and hence there is no anatomical basis of cross connection between the olfactory bulbs and their cerebral centres.

Though the lower end of the temporo-sphenoidal lobe is capable of being reached for purposes of isolated irritation with the electrodes, the operations necessary to display it are of such a severe character as to render complete exposure of it for purposes of localised disorganisation incompatible with the conditions of continuous or trustworthy observation afterwards. I have, therefore, not attempted exact circumscription of the lesion, but have destroyed the subiculum from a point comparatively easily exposed, but necessitating more or less extensive lesion of the other convolutions of the temporo-sphenoidal lobe. By exact limitation, however, of the lesion in other instances, the other sensory centres have been determined, and the complex effects of undefined lesions of the temporo-sphenoidal lobe have been analysed, and referred to their separate cause by a process of exclusion. Already the centres of sight, hearing and touch have thus been circumscribed and determined. The centres of smell and taste now remain to be similarly fixed.

In the first experiment made in reference to this point, the lower part of the left temporo-sphenoidal lobe was severed, and almost completely removed, the loss of substance extending to the hippocampus and uncinate convolution, the free surface of which, however, remained continuous and unbroken.

The lesion was such as to sever the connections of the lower end of the temporo-sphenoidal lobe, and to disorganise it to a very considerable extent, though not completely. Owing to the superior temporo-sphenoidal convolution being disorganised, hearing was diminished or abolished on the right side. The reaction to the vapour of acetic acid was less marked in the left nostril than in the right, though not abolished. As regards taste nothing very definite could be made out, owing to the diffusion of substances placed on the one side of the tongue to the other, but the reaction was diminished on the right side. Sight remained unaffected, but tactile sensibility became less acute on the right side, owing to the fact of the hippocampus, as softening advanced, becoming to some extent involved in the lesion. In a second similar experiment on the left side, the division of the lobe was carried so deeply as to cause considerable disorganisation of the hippocampus major, and almost complete separation of the lower part of the temporo-sphenoidal lobe from the rest. At the same time the superior temporo-sphenoidal convolution was disorganised.

Hearing, as determined by absence of reaction when the left ear was stopped, was abolished on the right; tactile sensation was at first impaired, and ultimately almost completely abolished on the right side, whilst sight continued unimpaired;—effects attributable to the lesion of the superior temporo-sphenoidal and the hippocampus respectively, and the absence of lesion in the angular gyrus. Taste was not experimented on, on account of the difficulty of drawing accurate conclusions from unilateral lesions. As regards smell, which was tested before tactile sensation became impaired, the following circumstances seemed to point to diminution or loss. When a piece of apple was offered the animal took it, smelt it, and began to eat. The right nostril was then securely plugged with cotton wool. After this a piece of apple was again offered to it. The animal took it, but hesitated before eating, raising it repeatedly to the nostril, and endeavouring to smell it, apparently without success: facts evidently indicating that smell was affected on the left side.

In a third experiment the temporo-sphenoidal lobes were divided transversely on both sides, and the substance of the lobes disorganised by the cautery below the section. Tactile sensation ultimately became affected on both sides, more on the right than left, facts which coincided with softening of the hippocampus both on the left and right, but especially on the left.

Acetic acid caused no reaction when held close to its nostrils, or placed in its mouth. When the acetic acid was placed within the nostrils reaction occurred, an effect due to irritation of the sensory branches of the fifth, distributed to the mucous membrane. Smell and taste, therefore, in this case, also, were shown to be affected by lesion of the lower part of the temporo-sphenoidal lobe.

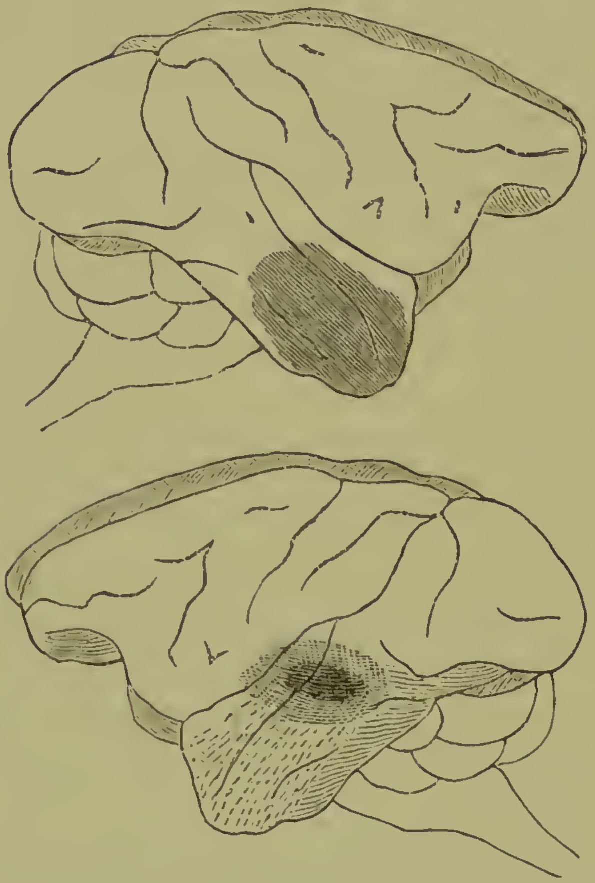
The following experiment, however, made with the purpose of restricting the disorganisation as much as possible to this region, is more conclusive as regards taste and smell.

In this case the superior and middle temporo-sphenoidal convolutions on both sides were sufficiently exposed to allow of the introduction of the cautery downwards and forwards, so as to disorganise the lower part of the temporo-sphenoidal lobe. This, as was ascertained *post mortem*, was done so effectually as to destroy the region of the subiculum and neighbouring parts of the lower temporo-sphenoidal convolutions completely on both sides, and also on the left side to disorganise the hippocampus (see figs. 50 and 51).

Tactile sensibility, owing to the destruction of the hippocampus, was abolished on the right side of the body, face, hand and foot, the animal ceasing to use these limbs, and not reacting to cutaneous stimuli which excited active manifestations on the left side. Sight was retained unimpaired.

Neither aloes nor colocynth, nor citric nor acetic acid, which in ordinary conditions excite lively indications of disagreeable sensation in the monkey, caused the slightest appearance of reaction when placed on the tongue. Acetic acid held close to the nostrils, caused no reaction. Introduced with a feather within the nostrils, a remarkable difference was observable in the reactions of the right and left respectively. On the right side, which was also devoid of cutaneous sensibility, the acetic acid caused no reaction of any kind, and no lacrymation. On the left side no motor reaction ensued, but copious lacrymation, from the left eye particularly.

These results were determined by careful and repeated trials. The tongue, moreover, was not only insensible to sapid stimuli, properly so called, but also to cutaneous stimuli. While the animal was lying half asleep with the tongue slightly protruding between the teeth, the application of pungent heat caused no reaction. The application of the same stimulus to the left hand caused sudden awakening and active withdrawal of the hand. The facts of this experiment show that with the disorganisation of the lower part of the temporo-sphenoidal lobe, smell and taste are abolished. The lacrymation which resulted from the introduction of a pungent vapour within the nostril was due to reflex reaction through the sensory branches of the fifth nerve, for in the nostril in which there was cutaneous as



Figs. 50 and 51.—Lesions of the Right and Left Hemisphere, causing loss of taste and smell. (Roy. Soc.) In the right hemisphere (50) the shading indicates the extent of destruction of the grey matter. In the left (51) the dark shading indicates the superficial extent of the wound; and the dotted lines the extent of internal destruction of the lower portion of the temporo-sphenoidal lobe.

well as olfactory anæsthesia, no such effect was produced; while in the other, deprived of olfactory sensibility, but retaining common sensibility, this effect was marked. With the abolition of taste cutaneous sensibility of the tongue was also abolished, a fact indicating the association in the hemisphere of the centres of tactile and special sensation in the tongue. Owing to the destruction of the right hippocampus the loss of tactile sensation on the left side is easily accounted for, but as in the right hemisphere only the lower part of the hippocampus was disorganised without causing general cutaneous anæsthesia on the opposite side, the lesion must have affected the centres both of the tactile and gustatory sensibility of the tongue.

§ 70. None of these experiments serve to define the exact limits of the regions of taste and smell respectively. Other considerations, however, chiefly founded on the effects of electrical irritation, serve to localise more especially the region of smell. Electrical irritation of the subiculum causes phenomena clearly associated with excitation of olfactory sensation, and this region is therefore to be regarded as that specially related to smell. The comparative development of this region in animals in which the sense of smell is largely developed, as in the dog, cat and rabbit, strongly bears out this view.

As regards taste, I think that the phenomena occasionally observed in monkeys on irritation of the lower part of the middle temporo-sphenoidal convolution, *viz.*, movements of the lips, tongue and cheek pouches, may be taken as reflex movements consequent on the excitation of gustatory sensation. The abolition of taste coincided with destruction of regions situated in close relation to the subiculum. It is probable, also, that the movements of the jaws observed in cats on irritation of the temporo-sphenoidal lobe posterior to the fissure of Sylvius (§ 56) are also of the nature of reflex indications of the excitation of gustatory sensation.

The localisation of the centres of smell and taste in close relation to each other in the lower portion of the temporo-sphenoidal lobe at once receives support from, and throws considerable light on, certain curious clinical cases which occasionally present themselves to the physician.

It is a well-established fact, that blows on the head, particularly on the vertex or occiput, are sometimes followed by temporary or permanent loss of the senses of taste and smell, the more immediate effects of the injury being completely recovered from.

Cases of this kind have been recorded by W. Ogle ('Med. Chir. Transactions,' 1870) and others. And quite recently, a case of this sort came under my own care at King's College Hospital. The patient in question had entirely lost taste and smell in consequence of a fall on the top of his head from a cart into the paved street. With the exception of anosmia and ageusia, all other evil effects of the injury had long disappeared. Ogle is inclined to regard the loss of taste as simply due to the loss of smell which forms an essential factor in the discrimination of so many flavours. But in the patient to whom I refer the explanation is not applicable, for taste was entirely abolished even for such radical contrasts as sweet and bitter. Smell properly so called was entirely abolished, acetic acid was not perceived, but ammonia caused a pungent or prickling sensation in the nostril and copious lacrymation, but none of that active retraction of the head which it produces in a normal individual.

Under the influence of treatment taste became improved, so that the patient could readily discriminate between sweet and bitter, and even between the flavours of beef and mutton. Smell, however, remained absolutely annihilated, a fact which shows that the return of taste was not due to a coincident improvement in the sense of smell.

As regards causation, it is in the highest degree improbable that a blow on the head could cause a simultaneous injury or rupture of such widely-separated nerves as the olfactory, the gustatory, and the glossopharyngeal. Ogle has suggested the true method of causation, *viz.*, injury by counter-stroke to the antero-inferior parts of the cerebral hemispheres. He, however, attributes the symptoms to rupture of the olfactory nerves in their course from the bulb through the ethmoid into the nostrils. This may account for pure loss of smell of a permanent character, but is inconsistent with the cases of recovery and with the undoubted independent association in some cases of loss of taste with the loss of smell.

While I regard the cause of the symptoms to be injury by counterstroke, I attribute them to lesion of the lower part of the temporo-sphenoidal lobe, where the centres of taste and smell are localised in immediate relation to each other. The lesion may be of a permanent or temporary nature, and the symptoms will remain or disappear accordingly.

Another interesting confirmation of the localisation of the sense of smell in this region, and further, of the important fact of the direct relation of this centre to the nostril of the same side, is furnished by the occurrence of unilateral anosmia with aphasia and right hemiplegia. Two such cases are recorded by Ogle *(op. cit.)*; one such is related by Fletcher and Ransome ('Brit. Med. Jour.,' April, 1864), and similar cases are given by Hughlings-Jackson ('London Hosp. Reports,' vol. i. p. 410).

As the cerebral lesions in these cases were undoubtedly in the neighbourhood of the island of Reil, and the margins of the fissure of Sylvius, the extension of the softening to the region of the subiculum gives a satisfactory explanation of the symptoms. In all the cases recorded, the anosmia was on the same side as the cerebral lesion causing the aphasia and dextral paralysis. How, then, are we to account for the symptoms observed in cerebral hemianæsthesia? In this condition the loss of smell is observed on the same side as the cutaneous anæsthesia, *i.e.*, on the side opposite the lesion. The true explanation seems to me to be furnished by the well-known experiments of Majendie ('Leçons sur les Fonctions et les Maladies du Système Nerveux,' tome ii. 15e leçon, etc.) on the functions of the fifth nerve. Majendie found that smell was lost when, by reason of division of the sensory branches of the fifth, the sensibility of the nostril was completely abolished. These experiments did not prove that the fifth was the nerve of smell properly so called, but that the integrity of the fifth was necessary to the due functional activity of the olfactory nerves. In a case reported by Magnan, smell progressively diminished with the diminution of tactile sensibility in the nostril, and disappeared *pari passu* with it. The loss of smell was, therefore, of the same nature as that caused by direct division of the sensory branches of the fifth nerve. Even, however, when tactile sensibility was entirely gone in the nostril, the vapour of acetic acid caused copious lacrymation, a fact which shows that some afferent fibres still remained functionally active in the nostril, evidently the olfactory nerves, which, however, owing to the loss of common sensation, were not of themselves sufficient to convey the impressions of odours. In the monkey in which both tactile and olfactory sensibility was abolished in one nostril by cerebral lesion, lacrymation was not caused by acetic acid. In the other nostril, in which tactile sensibility remained, but olfactory was abolished, acetic acid excited lacrymation, a reflex reaction through the fifth, but not excluding the possibility of a similar reflex relation between the olfactory and the secretory nerves of the lacrymal gland. This latter seems to account satisfactorily for the lacrymation in Magnan's case.

The Occipital Lobes.

§ 71. Electrical irritation has not as yet succeeded in furnishing any clue to the interpretation of the function of the occipital lobes in the monkey. The results, as far as outward manifestations are concerned, have always been negative in the numerous cases I have experimented on. Though specially differentiated occipital lobes are not to be found in the brain of the dog, cat, etc., yet the posterior extremities of the cerebral hemispheres in these animals physiologically resemble the occipital lobes of the monkey, in failing to react to electrical irritation.

Nor are the effects of limited destruction of the occipital lobes such as to throw clear positive light upon their physiological significance. Negatively, however, this method of experimentation establishes facts of the utmost importance. In five instances in which I disorganised the occipital lobes more or less completely on both sides, sometimes removing them *en masse*, the animals, notwithstanding the mutilation, retained all their powers of voluntary motion, and with the exception of some affection of vision, due to other causes, retained all the faculties of special sense unimpaired.

One or two animals from which the occipital lobes had been removed by a line of separation trenching closely on the posterior limb of the angular gyrus, suffered from impairment of vision, and ultimately became quite blind. In these cases it was found that the division by the cautery, or the subsequent occurrence of inflammatory softening, combined with the hernial protrusion of the cut surface, had seriously involved, or altogether disorganised the angular gyrus, which, as has been seen by former exact experiments, is the centre of vision.

Excluding this complication, it may, therefore, be stated absolutely that the removal of the occipital lobes is without effect on the faculties of special sense or the powers of voluntary motion. The animal continues to see, hear, touch, taste, and smell as before; and can walk, run, jump, and use its limbs with perfect power and co-ordination. The functions of circulation and respiration are likewise unaffected.

This remarkable absence of symptoms in the domain of the special sensory and motor functions of the body, renders it difficult to attach any definite physiological significance to the occipital lobes.

But the removal or disorganisation of the occipital lobes was not altogether without influence on the bodily and mental condition of the animal, and this of such a kind as to suggest important inferences or hypotheses as to their function. It is an extraordinary and, to many, scarcely credible fact, that the severe operations of trephining the skull, and exposure and removal of considerable parts of the brain substance, should exercise very little disturbing influence on the animals' bodily health. But within a few hours after the operation they eat and drink, and appear (with the exception of the special sensory or motor paralysis, or other limited effect) in normal condition. This state continues until inflammatory processes begin to be lighted up and to extend, but several days may intervene before the constitutional disturbance is such as to derange to any appreciable extent the animals' sense of well-being or appetite for food or drink. I have in the course of my investigations practically removed every part of the cerebral hemispheres, but beyond the special affections of motion and sensation attributable to the destruction of special centres, I have never seen such affection of the appetite for food as results from destruction of the occipital lobes. This is not due to the mere severity of the operation, for the removal of the occipital lobes is, perhaps, more easily effected than removal of any of the sensory or motor centres. The removal of the frontal lobes is as severe an operation, and perhaps more so, than removal of the occipital lobes; yet after removal of the frontal lobes the animals retain their appetite, and eat and drink with apparently as much relish as before. After removal or disorganisation of the occipital lobes the appetite for food is abolished, the animals refusing that which formerly they exhibited a great liking for. This I have tested in various animals, and in various ways. The appetite for drink, however, still remained, for nearly all the subjects of my experiments took water offered them, or found it for themselves, when they could not be prevailed upon to eat. Along with this refusal of food the animals generally exhibited a condition of depression and apathy, and, in general, rapidly succumbed. A very remarkable exception, however, occurred, tending apparently to overthrow any conclusions which might seem warranted by the condition manifested by the others.

In this animal, from which the occipital lobes were separated and removed by a line passing vertically through the anterior extremity of the superior occipital sulcus (fig. 26, *o*), complete recovery took place, the only instance I have seen of the kind after such operations on the brain. Like the other animals so operated on, the animal refused to eat, but drank water occasionally. This refusal of food continued five days, the animal having only sucked a piece of orange or two, which it accepted, refusing all its formerly favourite dishes. During the above period it used to run about with a companion monkey, of which it had constituted itself protector, and exhibited unmistakable signs of anger when anyone else touched it.

At the end of the fifth day, after trying to tempt it with various kinds of food, I offered it a cold potato. This it took, smelt several times, and at last, as if struck by a new idea, began to eat with great relish. From this time it began to take food regularly, and recovered. As regards the animal's mental condition, only some degree of apathy and general indifference was observed, it having been formerly a very lively and intelligent monkey. Some defect of vision also existed, not of such a nature, however, as to interfere with its usual modes of activity, but shown particularly in incorrect appreciation of distance. On *post-mortem* examination it was found that the angular gyri were partially affected by the lesion.

Notwithstanding the recovery of the one animal, I am clearly of opinion, from an extensive observation of the effects of localised destruction of various regions of the cerebral hemispheres, that there is a causal relation between the removal of the occipital lobes and the annihilation of the appetite for food. On analysis of the conditions of hunger and thirst, we find that the proximate cause of the sensation of thirst is a dry condition of the fauces, which is the local expression of the general bodily need of water. The dry condition of the fauces is a purely tactile sensation. In cerebral hemianæsthesia, besides the cutaneous surfaces, the mucous membranes of the mouth and nostrils are rendered quite anæsthetic. Removal of the occipital lobes, however, does not affect tactile sensibility either of the skin or mucous membranes of the orifices of the body; hence the conditions for the local manifestation of thirst remain, and the appetite for drink is not necessarily affected.

The conditions of the appetite for food are, however, different from those of thirst.

The proximate cause of hunger is a local condition of the stomach, and the sensation in this case belongs to the truly organic sensations. The organic, or visceral, sensations form a group distinct from the tactile, or cutaneous. This is shown by the fact that when, as in cases of cerebral hemianæsthesia, tactile sensibility to all kinds of stimuli is abolished in the skin and limbs, deep pressure exerted on the liver, kidneys, ovaries, or internal viscera causes the same pain as in normal conditions. As a general rule the states of the viscera do not rise into distinct consciousness, except when the condition is extremely abnormal, as in inflammatory affections. In such cases pain may be more or less accurately referred to the viscus affected, but more generally morbid states of the viscera express themselves through other sensory nerves, often at a distance from the seat of the malady, by what is termed sympathy, or synæsthesia. Thus morbid conditions of the reproductive organs often manifest themselves in infra-mammary neuralgia, and abnormal states of the stomach and intestines in neurosis of the fifth nerve, as in headache, toothache, and the like.

But though the viscera, except in extreme conditions of disease, have no very definite expression in consciousness, they form the chief foundation, according as they are healthy and vigorous, or depressed and morbid, of that indefinable and non-localisable feeling of well or ill being, with which everyone is familiar.

In so far as these systemic sensations, conveyed by the pneumogastric and sympathetic, are capable of being distinctly localised, as in hunger, and in so far as they form the basis of the vague feelings of joyousness or depression, or the foundation of obscure longings, they must be represented in the cerebral hemispheres, or centres of consciousness and memory, and in all probability in the occipital lobes. I doubt much whether experimental physiology is competent to solve the problem definitively, involving, as it does, so much of the purely subjective.

But the evident affection of one of the systemic sensations, by destruction of the occipital lobes, argues in favour of the hypothesis which I have advanced. Anatomically, also, the occipital lobes stand in relation to the sensory tracts of the cerebral peduncle, and the hippocampus minor may be regarded as merely an offshoot from the hippocampus major. This latter, as has been shown, is related to tactile sensation, and as there is great similarity between this and the visceral sensations, the hypothesis as to the functions of the occipital lobes is supported both by physiological and anatomical considerations.

The chief objection to the view that the occipital lobes are related to the systemic sensations, and one which I am not disposed to underrate, is the fact, already mentioned, that the monkey which recovered from the removal of the occipital lobes began again to take food after five days of abstinence. If the occipital lobes are the centres of the sensations on which hunger depends, how can the apparent return of appetite be accounted for, in an animal from which these centres have been removed? Supposing the relation of the occipital lobes to the feeling of hunger established, is it possible for the remaining parts of the brain to take up and compensate for the functions of the centres which have been lost? Those who believe in the qualitative and quantitative equivalence of the various parts of the brain might readily answer this question in the affirmative. Evidence, however, has been given, and more will be furnished, that this doctrine, which is in direct opposition to the localisation of specific function, is incapable of being maintained.

It is possible, however, that by a process of association, functions primarily and chiefly dependent on certain parts, may, though temporarily suspended by destruction of these parts, again become manifested. Though the ingestion of food is primarily dependent on the sensation of hunger, yet food is associated powerfully with smells and tastes, so that the well-known sight of food, in combination with well-known odours and the taste arising from its introduction into the mouth, and all these added to the automatic or mechanical link between the sight or smell of food and eating it, might come to compensate for the loss of the sensation on which the acts of searching for and ingestion of food primarily depended. That some such link of association was established in the monkey referred to (p. 194) is, I think, indicated by some of the facts observed. The first appearance of desire for anything beyond water was when a piece of orange, appealing strongly to smell and taste, was offered. This, however, might be more correctly referred to the gratification of thirst rather than of hunger. But at the end of the fifth day, though ordinary food failed to tempt the animal, the appearance and smell of a potato, carefully examined, seemed to inspire a new idea, and led to the regular taking of food.

I am far from regarding the evidence adduced in support of the relation of the occipital lobes to the visceral sensations as of the same weight as that relating to the localisation of regions of special sense. Further investigation by new methods, aided by careful clinical and pathological observation, may serve to throw more light on a very obscure subject.

The consideration of the visceral sensations naturally suggests that of the sexual appetite. In the course of the observations on the monkey whose occipital lobes had been removed, and which ultimately recovered, I noted certain phenomena which clearly indicated that the sexual appetite had not been abolished by the lesion. On the third day after the operation the animal was observed on two separate occasions to seize its companion monkey in sexual embrace. This occurred at a time when the animal had not as yet recovered its appetite for food, and was an act hardly consistent with that physical prostration and constitutional disturbance which to some might appear more likely to account for the anorexia than the special lesion of the occipital lobes.

The importance of the phenomenon lies as much in its manifestation at all, as in indicating that the occipital lobes are not the seat of this feeling. The excitation of the appetite cannot have arisen *ab extra* in the usual manner, for the companion monkey was also a male, and resented the proferred embrace. It would therefore seem to have been caused by central irritation, and the conditions were such as to excite by inflammatory irritation the centres of the sexual feeling, supposing these to be in immediate contiguity to the line of section of the occipital lobes. The organic wants which form the basis of the sexual appetite (p. 262) centre round a special form of tactile sensation, and this may be supposed to have its centre in close relation to the hippocampal region. Further, as is well known, one of the most powerful excitants of the sexual appetite in the lower animals is a special sexual odour, and though in man the excitation of the sexual appetite by smell is not so apparent, yet it is considered by some, and with great probability, that the fondness for certain odours, especially musk, its congeners and derivatives, is closely allied to the erotic instinct (Laycock, 'Nervous Diseases of Women,' 1840). A region, therefore, in close relation to the centres of smell and tactile sensation might be regarded as the probable seat of the sensations forming the basis of the sexual appetite. The occipito-temporal convolutions, or those connecting the lower and inner part of the temporo-sphenoidal with the occipital lobe, would fulfil these conditions, and at the same time are so situated as to have been irritated by the inflammatory processes set up by section of the occipital lobes. The value of this hypothesis I leave to be tested by further physiological and pathological research.

SECTION II.—THE MOTOR CENTRES.

§ 72. It has been shown in the preceding chapter (Chap. viii.) that electrical irritation of the brain of the monkey at certain definite points in the convolutions, which, speaking generally, bound the fissure of Rolando, gives rise to certain definite and constant movements of the hands, feet, arms, legs, facial muscles, mouth and tongue, etc. Similar, and in many respects completely homologous movements, were shown to result from irritation of the frontal regions of the external convolutions in the brain of the cat, dog and jackal, and of the anatomically corresponding frontal regions of the smooth brain of the rodents; the regions characterised by similarity of movements having been indicated in the figures and description by the same letters of designation.

As a basis of topographical homology between the brain of the monkey and the lower vertebrates, these data have an important value. The motor regions of the brain of the monkey are situated farther back than the corresponding regions in the lower animals, occupying more properly the parietal than the frontal lobes. The fissure of Rolando of the monkey is shown, by the homology of the centres surrounding it, to correspond to the crucial sulcus of the carnivorous brain. This is an important landmark by which we may determine the respective development of the frontal region proper in these various animals. In the brains of the carnivora the centres in advance of the crucial sulcus become reduced to very small dimensions as compared with the frontal convolutions of the brain of the monkey; these are insignificant in turn, when compared with the homologous parts of the human brain.

The convolutions in the brain of the monkey are so disposed that it is not easy to trace any resemblance between them and the external convolutions of the carnivorous brain, which run almost parallel to each other from the frontal to the posterior extremity of the hemisphere. If, however, the fissure of Rolando, instead of extending so far downwards, were to terminate abruptly on a level with the supero-frontal sulcus (fig. 26, *s f*), it would be possible to trace a superior external convolution, as in the dog, commencing with the superior frontal convolution, doubling the fissure of Rolando in a sigmoid curve, formed by the upper extremities of the ascending frontal and ascending parietal convolutions, into the postero-parietal lobule, and thence into the occipital and temporo-sphenoidal lobe. So also, if it were not interrupted by the antero-parietal sulcus (fig. 26, *a p*), a continuity might be traced, as in the second external convolution of the dog, between the second frontal and the angular gyrus. And a third continuous convolution might be found in the lower frontal on the one part, and the superior temporo-sphenoidal on the other.

The question, however, with which we are more particularly engaged is the determination of the physiological significance of these regions. The mere fact of the excitation of movements is, as we have already seen, no proof that the regions stimulated have a motor significance, for the stimulation of a sensory centre may give rise to reflex or associated movements. Whether the centres now under consideration are directly motor, or only give rise to movements in a reflex or indirect manner when stimulated, is a question which has been answered differently by different investigators on this subject. The definite purposive character clearly perceivable in many of the movements, and their correspondence with the ordinary volitional activities and peculiarities of the animals, apart from other considerations, point rather to the conclusion that they are the result of the artificial excitation of the functional activity of centres immediately concerned in effecting volitional movements, and as such truly motor. As the question, however, is one capable of being answered by direct experiments, we may proceed to the consideration of these. If these regions are centres of voluntary motion, paralysis of voluntary motion ought to follow from their destruction, and any apparent exception to this result must be capable of satisfactory explanation, consistently with this view, if it is the correct one.

The following experiments on monkeys give no uncertain reply to the questions stated.

The first experiment I have to record is instructive, as showing the respective effects of irritation and destruction of the convolutions bounding the fissure of Rolando. The right hemisphere of a monkey had been exposed and subjected to experimentation with electrical irritation. The part exposed included the ascending parietal, ascending frontal, and posterior extremities of the frontal convolutions. The animal was allowed to recover, for the purpose of watching the effects of exposure of the brain. Next day the animal was found perfectly well. Towards the close of the day following, on which there were signs of inflammatory irritation and suppuration, it began to suffer from choreic spasms of the left angle of the mouth and left arm, which recurred repeatedly, and rapidly assumed an epileptiform character, affecting the whole of the left side of the body. Next day left hemiplegia had become established, the angle of the mouth drawn to the right, the left cheek-pouch flaccid and distended with food, which had accumulated outside the dental arch; there being almost total paralysis of the left arm, and partial paralysis of the left leg. On the day following the paralysis of motion was complete over the whole of the left side, and continued so till death, nine days subsequently. Tactile sensation, as well as sight, hearing, smell and taste, were retained. On *post-mortem* examination it was found that the exposed convolutions were completely softened, but beyond this the rest of the hemisphere and the basal ganglia were free from organic injury (fig. 52).

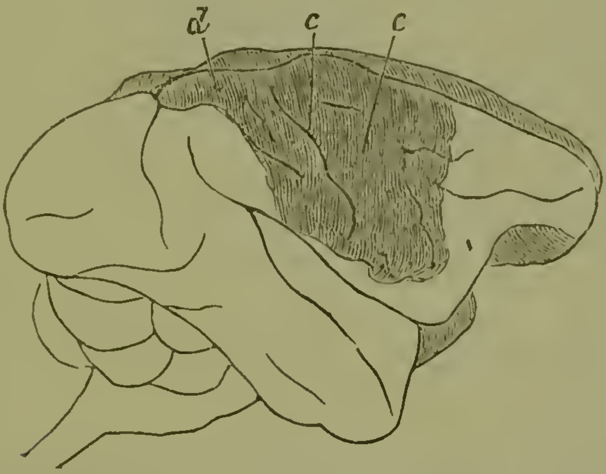


FIG. 52.—Lesion of the Grey Matter of the Right Hemisphere, causing complete hemiplegia of the opposite side without affection of sensation. (Roy. Soc.) *c*. The fissure of Rolando. *d*. The postero-parietal lobule. *e*. The ascending frontal convolution.

In this we have a clear case, first, of vital irritation producing precisely the same effects as the electric current, and then destruction by inflammatory softening, resulting in complete paralysis of voluntary motion on the opposite side of the body, without affection of sensation.

In the next experiment the lesion was more limited, and the state of paralysis was limited correspondingly. The left hemisphere of a monkey was exposed, and the cortical substance destroyed by the cautery in the postero-parietal lobule (foot centre), ascending parietal convolution (hand and wrist movements), and superior part of the ascending frontal convolution (movements of arm and leg) (see § 53, fig. 29). The centres of the biceps, facial muscles, and mouth and tongue were not involved. Immediately on this being done the right leg was found to be dragged, the foot and ankle especially hanging flaccid and powerless.

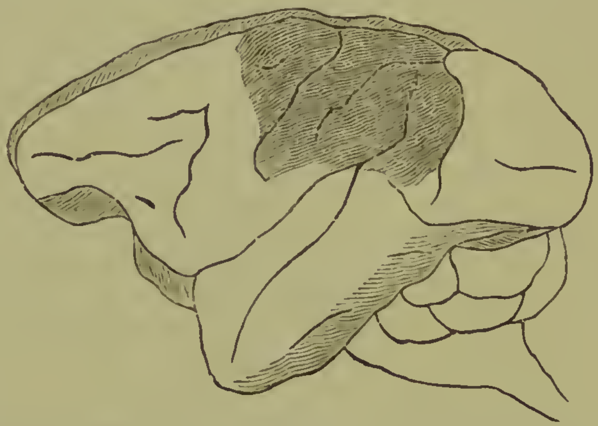


FIG. 53.—Lesion of the Left Hemisphere, causing motor paralysis of the right leg and right hand and wrist, and of some of the movements of the right arm, and loss of sight in the right eye. (Roy. Soc.)

The right hand and wrist hung powerless and flaccid, but the animal could flex the forearm and maintain resistance against extension, a fact easily accounted for by the biceps centre remaining intact. There was no trace of facial paralysis or distortion of the angle of the mouth. Cutaneous sensation and the various special senses were unimpaired, and beyond the paralysis mentioned the animal was in good condition, and enjoyed food. In this animal the angular gyrus was subsequently destroyed, with the effect of causing blindness of the right eye.

On *post-mortem* examination next day the lesion was found to occupy the motor regions specified and the angular gyrus, the rest of the brain and the basal ganglia being intact (fig. 53).

In this case the paralysis was confined to the same movements as result from electric stimulation of the centres specified. In the following experiment the extent of the lesion was still further circumscribed, and the effect, as regards voluntary motion, correspondingly limited.

The left hemisphere of a monkey was exposed in the region of the ascending frontal convolution sufficiently to display (6) (fig. 29), the centre of bicipital action, or supination and flexion of the forearm. The exact spot being determined by the application of the electrodes, it was then accurately cauterised, just sufficiently to destroy the cortical grey matter. This operation immediately manifested itself in paralysis of the power of flexing the right forearm. All the other movements of the limbs were retained, but when the right arm was placed in an extended position the animal was utterly powerless to flex it, and the limb hung in a state of flaccid extension when the animal was lifted.

FIG. 54.—Lesion (*f*) of the Left Hemisphere, causing paralysis of the action of the biceps on the right side. (Roy. Soc.)

It raised things to its mouth with the left hand, the movements of the legs were intact, there was no facial paralysis, and cutaneous and other forms of sensation were unimpaired.

As the animal died from an overdose of chloroform, some hours after, when it was being narcotised, observations on the degree of permanency and subsequent course of the phenomena were cut short. On *post-mortem* examination the lesion was found exactly limited to the point above indicated, the rest of the brain being perfectly normal (fig. 54).

To these experiments I might add others, in which, from extension of the lesion, at first circumscribed to the sensory centres (angular gyrus, etc.) some limited paralysis exhibited itself, as of the wrist and hand. Such cases always coincided with softening of the respective motor centre, as already determined by the electrical exploration. In all cases, so long as observation could be maintained, the progress, as regards the paralysis, was always from bad to worse, there being no appearance of compensatory action, or return of the faculty of movement when the centre was effectually disorganised. No evidence could to my mind more convincingly prove that destruction of the cortical substance of what we may justly term the motor centres in the monkey causes paralysis of the movements determined by the electric stimulus, and that this paralysis is entirely dissociated from sensory paralysis in any form. It has been shown that paralysis of tactile sensation may cause paralysis of motion, by abolishing that which is the usual guide to muscular movement. In these experiments the power of movement alone was destroyed, sensation remaining acute and unimpaired.

As to the duration of the motor paralysis in the monkey from lesions of the cortex, owing to the impossibility of continuing observations beyond a comparatively limited space of time, little more can be said than that there is no appearance of reparation or compensation during such time as the animals can be kept alive. On this point, however, human pathology supplies that which experimental physiology lacks. Numerous cases might be given where, from softening of the cortex of the hemisphere invading the homologous motor regions of the human brain, permanent hemiplegia has resulted. As an instance, I would refer to a case reported by Lépine in his admirable memoir 'De la Localisation dans les Maladies Cérébrales,' Paris, 1875. The case is described under the heading (p. 33), 'Destruction Totale (large plaque jaune) de la Circonvolution Pariétale Ascendante ; Partielle du Lobule de l'Insula, de la Circonvolution Frontale Ascendante, des Lobules Pariétaux supérieur (postero-parietal lobule) et inférieur. Intégrité Absolue de la Couche

Optique et du Corps Strié; Hémiplégie Permanente et Dégénérations Descendantes Consécutives.' In this case, in which the regions corresponding to the motor centres of the brain of the monkey were disorganised, there was hemiplegia of the opposite side, lasting six years. The motor tracts of the pons on the same side, and of the anterior pyramid on the opposite side, had undergone atrophy in a line corresponding to the outward transmission of motor impulses from the hemisphere. The various forms of sensibility remained intact and unimpaired.

Another case, carefully observed, is recorded by Gliky ('Deutsches Archiv für Klin. Med.,' Dec. 1875). The patient, after suffering from unilateral convulsive attacks on the left side of the body, became afterwards completely hemiplegic on that side, without affection of sensation. After death a caseous degeneration was found to involve the motor centres in the right hemisphere, *viz.*, the ascending frontal and posterior extremities of the three frontal convolutions, the ascending parietal and postero-parietal lobule. Part of the supro-marginal convolution was also involved in the lesion (see description of fig. 27). Various other similar cases might be cited of limited paralysis on the opposite side of the body, from partial lesion of the cortex of the opposite hemisphere, without affection of the basal ganglia or peduncular tracts. In man, therefore, disorganisation of the cortical centres, which are termed motor, causes lasting paralysis of voluntary motion on the opposite side of the body, a fact which experiments on the monkey would have led us to expect.

§ 73. When, however, we turn from the monkey to the lower animals, the cat, dog and rabbit, we meet with facts which to some appear irreconcilable with the view that the homologous centres in these animals have a motor signification.

Nothnagel (Virchow's 'Archiv,' Band lvii.) has studied the effects of destruction by injection of chromic acid into circumscribed regions of the hemispheres in rabbits. Hitzig, in addition to the investigations which he made with his colleague Fritsch, has undertaken a new series of experiments on dogs, destroying the centres by extirpation of the grey matter ('Reichert's und Dubois Reymond's Archiv,' 1874, p. 392). Similar experiments have been made by Schiff ('Archiv für Experiment. Path. u. Pharm.,' Band iii. 1874), and by Hermann ('Pflüger's

Archiv f. Physiologie,' Band x. 1875). The admirable memoir of Carville and Duret ('Sur les Fonctions des Hémisphères Cérébraux,' 1875) contains the most elaborate series of experiments and the ablest exposition of the effects of destructive lesions of the motor centres in dogs.

The centres for the movements of the limbs in dogs are, as has been shown, situated in the sigmoid gyrus (fig. 32).

When these are destroyed, whether by excision or by cauterisation, the movements of the opposite limbs are immediately affected in a very marked manner If the centres of the left hemisphere have been destroyed, the animal, on attempting to stand, falls over on the right side, the limbs doubling up under the animal in a powerless manner. There is no absolute motor paralysis, however, as in the monkey, for the animal soon succeeds in getting on its feet, but the right limbs tend to deviate and give way, so that the animal slips, stands on the dorsum of its foot, or plants it in various abnormal postures. Walking, at first impossible, is soon attempted, the animal continually tending to fall, and frequently actually falling, especially if its movements are at all hurried. Gradually, however, the power and control of the limbs improve so that, unless on any sudden movement, when the weakness of the left side is clearly manifested, it would be difficult to detect any affection of motility. Frequently within a few days, the effects, so marked at first, may have entirely, or almost entirely, disappeared. Ultimate recovery, if the animal does not die from encephalitis, occurs sooner or later in all. The paresis can be limited to individual movements, or to one limb, according as the lesion is exactly circumscribed in accordance with the position and extent of the centres previously localised by electric irritation. Of this fact Hitzig's experiments also afford numerous illustrations.

In all these cases of disorders of motility there is no indication, judging from sensory reaction, of impairment of sensibility in the limb. The affection is, therefore, one of motility and not of sensibility. In the cat the phenomena are essentially the same. In the rabbit the effects are even more transitory than in either cat or dog, as I have found by repeated experiments. Compared with similar experiments on the monkey, experiments on dogs agree in so far as that motion, and not sensation, is affected; but differ in this important particular, that the paralysis is less complete and is not enduring. The questions on which experimenters are not agreed are: what is the true cause of the affection of motility? and, how is the transitory nature of the affection to be explained?

I am clearly of opinion that the affection is essentially of the same nature as that which results from destruction of the homologous centres in the brain of the monkey, purely motor in character, and such as we may, with Carville and Duret, term, *paralysie de la motricité volontaire corticale.*

In order properly to understand the difference in degree of paralysis in the monkey and dog, it is necessary to revert to certain facts already alluded to in the first chapters of this work. As has been shown, the entire removal of the hemispheres operates differently in different classes and orders of animals. In the fish, the frog and the pigeon the removal of the hemispheres exercises little or no appreciable effect on the faculties of station and locomotion. Under the influence of stimulation from without, these animals swim, jump or fly with as much vigour and precision as before. In the rabbit the removal of the hemispheres, while decidedly impairing the motility of the forelimbs, does not quite destroy the power of station, or of co-ordinated progression in answer to external stimuli.

In the dog, however, the removal of the hemispheres exercises a much more marked influence on these powers, rendering station and locomotion absolutely impossible. Whether these might be regained in time, to some extent at least, is extremely probable, though difficult to determine experimentally, on account of the fatality of the operations necessary to decide this question. The independent or automatic organisation of the lower centres is thus seen to vary, according as we ascend or descend the scale. In proportion to the degree of independence, complexity and variety of the forms of motor activity of which the animal is ultimately capable, the more volitional and less automatic are its movements, and the longer is the period of infancy during which the animal is slowly acquiring volitional control over its limbs. Many of the lower animals start from birth with all their powers of movement already fully organised;

in most the period of helpless infancy is extremely short as compared with that of the simian or human young. In these every exact movement is the result of a long and laborious process of education. The more the movements are dependent on volitional control, the more marked and enduring is the paralysis resulting from destruction of the cortical centres or centres of voluntary motion. Hence, the complete and lasting nature of the paralysis from lesion of the cortical motor centres in the monkey and man. The more mechanical or automatic the movements are at birth, the less the disturbance exerted by destruction of the centres of voluntary acquisition. Hence, in the fish, frog and pigeon, the destruction of the cortical motor centres has little or no effect. Where voluntary control is speedily acquired, or automaticity inherited, or rapidly established, as in the rabbit and dog, the centres of voluntary motor acquisition may be removed without completely or permanently interfering with the powers of locomotion. Locomotion is still possible through the agency of the lower centres in which this mode of activity is mechanically organised, and may be set in action by various forms of external or internal impulse.

Besides these differences in the primary organisation of the nerve centres in different animals, there are certain facts of clinical observation in man, which have an important bearing on the mechanism of voluntary movements. In hemiplegia, or unilateral paralysis of voluntary motion from disease of the motor centres in the opposite hemisphere, it is found that the individual movements are not all equally affected; and further, that as the lesion, which has for the time annihilated the functional activity of these centres becomes repaired, the recovery of movement takes place in a certain order. Thus it is found that when the arm and hand are perfectly paralysed, some degree of voluntary control over the leg may still remain. The facial muscles are never so completely paralysed as in cases of disease of the *portio dura*, or special motor nerve of the muscles of expression. The eyelid in paralysis of cerebral origin can still be closed, though not so perfectly as that on the opposite side; while in facial or Bell's paralysis the eye remains permanently open, from complete paralysis of the *orbicularis oculi*. Generalising from these facts, it may be said that the more independent movements are most affected, while such movements as are usually associated in action with those of the opposite side—the eyelids, the facial muscles and leg—are less paralysed and more speedily recover. The varied and delicate independent movements of the hand are the last to recover the shock to the motor centres.

The limbs of quadrupeds are, as regards the character of their movements, more like the lower than upper limbs of man, inasmuch as they are capable of comparatively few independent movements, and, as a general rule, are exercised only in alternating or associated action with each other. This fact of bilateral association, taken with the fact of the greater degree of automaticity of the movements of the quadruped, serves to explain the partial and transient nature of the paralysis resulting from destruction of the cortical motor centres in these animals, as compared with the degree and duration of the effects of the same lesion in the monkey and man. The comparative escape of bilaterally associated movements in cases of hemiplegia is thus accounted for by Dr. Broadbent (' Brit. and Foreign Med. Chir. Review,' April 1866): 'Where the muscles of the corresponding parts on opposite sides of the body constantly act in concert, and act independently either not at all or with difficulty, the nerve-nuclei of these muscles are so connected by commissural fibres, as to be *pro tanto* a single nucleus. This combined nucleus will have a set of fibres from each corpus striatum, and will usually be called into action by both, but it will be capable of being excited by either singly, more or less completely according as the commissural connection between the two halves is more or less perfect.

'According to this hypothesis, then, if the centre of volitional action of one side is destroyed, or one channel of motor power is cut across, the other will transmit an impulse to the common centre, and this will be communicated to the nerves of the two sides equally if the fusion of the two nuclei is complete, and there will be no paralysis;—more or less imperfectly to the nerve of the affected side if the transverse communication between it and its fellow is not so perfect, in which case there will be a corresponding degree of paralysis' (*loc. cit.* Reprint, p. 11).

The explanation given by Dr. Broadbent of the comparatively slight affection of bilaterally associated movements in cerebral disease of the motor centres, while applying to the cortical motor centres which necessarily act downwards through the corpus striatum, is specially applicable to lesions situated in the corpus striatum and motor part of the cerebral peduncle.

Under the influence of one corpus striatum the conjoint mesencephalic and spinal centres are capable of being excited to action, according to the degree in which they are fused or welded together. This is entirely in harmony with the facts of clinical observation, and is capable of application to the associated movements of the limbs in quadrupeds. Something more, however, is needed to account for the transient nature of the paralysis in dogs, as compared with the permanent paralysis resulting from destruction of the cortical motor centres in the monkey and man. In the dog, as we have seen, apparently complete recovery may take place within a week after extirpation of the cortical centres, while the duration of the paralysis in the monkey and man is lasting or indefinite.

If we were to say, with Hermann, that the recovery in dogs disproves the view of the motor functions of the cortex, how shall we account for the paralysis observed in man and monkeys?

Assuming the motor functions of the cortical centres to be conclusively established, how are we to account for the rapid recovery in the one case and the permanent affection in the other?

Various explanations may be, and have been, given of these phenomena. It may be supposed that a process of compensation is effected by the corresponding cortical centres in the other hemisphere taking up the functions of those which have been lost. That the influence of the cortical centres and the corpus striatum of the other hemisphere plays an important part in the compensation, as far as regards the bilaterally associated movements is, I believe with Dr. Broadbent, unquestionable, and in harmony with clinical facts. It is observable, in cases of hemiplegia, that the patient, when told to raise the paralysed leg, is utterly unable to do so. If, however, he is asked to raise the sound leg, and *then* to raise the paralysed leg, a slight movement may be observed; and I have seen, when this alternate effort is persisted in, the paralysed leg raised to a considerable height. Here we have a clear instance of the volitional impulse of the sound hemisphere calling into play by association motor nuclei usually excited by the hemisphere which is diseased.

But the compensatory action of the cortical centres of the other hemisphere in respect of bilateral movements in man, is not sufficient to account entirely for the transient nature of the paralysis seen in dogs. If the compensation is effected by the cortical centres in the other hemisphere, it ought to follow that extirpation of these also in an animal which had recovered, should reinduce the paralysis which at first resulted from unilateral destruction of the motor centres. This, however, as Carville and Duret have shown, is not the case. In a dog, these experimenters removed the centres for the movements of the limbs in the right hemisphere. Paralysis ensued in the left limbs. After six or eight days the animal had recovered from the paralysis of the left side. The corresponding centres of the left hemisphere were then destroyed. This caused paralysis of the right limbs, but did not reinduce the paralysis of the left.

This experiment is sufficient to overthrow the theory of compensation by the motor centres of the opposite hemisphere.

But what may appear more difficult to reconcile with the motor function of the cortical centres, is the fact that even after disorganisation of the centres for the movements of the limbs in both hemispheres, the power of spontaneous movement of the limbs is not absolutely abolished. At first the animal makes disorderly struggles and vain attempts to get on its legs, which constantly give way under it; but after a time considerable improvement is observable, and ultimately the animal may succeed in standing tolerably securely, or even walking. These facts have been demonstrated by Carville and Duret, and though I have not succeeded in preserving animals until such complete recovery occurred, I can confirm the occurrence of spontaneous movements. How is this apparently voluntary control of the limbs regained after destruction of the supposed voluntary motor centres? Carville and Duret are of opinion that the compensation is effected by other parts of the hemispheres taking up the function of the parts which have been destroyed, and consider that these facts justify the formulation of a '*loi de la substitution functionelle*' of one part of the hemisphere by another, a hypothesis which coincides with the '*loi de suppléance*' of Flourens, Longet and Vulpian. It may, however, be pertinently asked why this functional substitution of one centre by another, if it has any real foundation, should not be manifested in the case of monkeys and man. If it is true at all, it ought to be true not only of cats and dogs, but also of monkeys. But the facts are entirely opposed to this view, for the paralysis resulting from destruction of the cortical motor centres in man and the monkey remains indefinitely. What, then, becomes of the law of functional substitution ? This hypothesis is in direct contradiction to the facts of specific localisation of function, demonstrated by the experiments above recorded and otherwise accepted by Carville and Duret themselves. If we were to suppose it possible that the functions of leg centres of the postero-parietal lobule could be taken up by the neighbouring angular gyrus, we should have the very remarkable substitution of a motor by a sensory centre, a region which is at one time a centre of visual sensation, becoming a centre of voluntary motion, or even a sensory and motor centre at one and the same time, if there is no break in the continuity of function. If the hypothesis had any foundation, we should equally expect the compensation of a sensory centre by a motor centre.

Such a mode of interpretation seems to me not a whit more justifiable than the supposition that the organ of sight might take up the functions of the organ of hearing, or that a nerve might at one time be a motor nerve and at another a sensory nerve, or perform both functions at once.

If, however, it is meant by this law of substitution that there is no direct establishment of new centres in place of those which have been lost, but that those which remain may indirectly, without assuming new functions, make up for the loss, to some extent at least, there is less objection to such a mode of representing the facts. In order to account for the retention of spontaneity and co-ordinated control of the limbs in dogs, after removal of the cortical motor centres, it is necessary to anticipate somewhat the consideration of the functions of the basal ganglia. (Further, *vide* Chap. X.)

Destruction of the corpus striatum (by which is meant both the ganglionic substance and the corresponding peduncular fibres) in the dog, causes hemiplegia of a very much more complete character than destruction of the motor centres of the cortex—a hemiplegia of apparently a persistent nature, just as in man and the monkey. The limbs hang flaccid, and the animal can neither support itself on its limbs nor use them in progression. In man, on the other hand, and in the monkey, the difference in degree of paralysis from destruction of the corpus striatum and from destruction of the cortical motor centres, is much less marked, and the duration is indefinite in both cases. In the rabbit, however, destruction of the corpora striata on both sides produces much less effect than in the dog, for the rabbit can still maintain its upright position, though the fore legs are weak and continually tend to give way and double up. The power of locomotion, however, is little interfered with, for the animal will, if stimulated, jump and spring repeatedly.

These differences are only to be accounted for on the principle already repeatedly enunciated, that the various classes of animals start from birth with different degrees of primary organisation of the powers of locomotion in the mesencephalic centres.

This automaticity is at its highest in the fish, frog and pigeon; to a less degree in the rabbit; and still less in the cat and dog; while in man it scarcely exists. The more the control of the limbs depends in the first instance, and continues to be dependent, on voluntary acquisition, the more does destruction of the cortical motor centres cause paralysis of movement. Hence in man and the monkey, in whom volition is predominant, and automaticity plays only a subordinate part in the motor activities, destruction of the motor centres of the cortex causes paralysis of a very marked character. In proportion, however, as movements at first requiring volitional education tend to become organised or rendered automatic, the less are they affected by injury to the cortical centres. Hence in the dog, in which the acquisition of the control of the limbs is speedy, the destruction of the cortical centres produces a much less marked effect; the movements having become in a great measure independent of these, through organisation in the subordinate centres.

The corpus striatum is the centre in which movements primarily dependent on volition proper tend to become organised.

That the individual centres which are differentiated in the cortex are integrated in the corpus striatum, is indicated by the experiments of Dr. Burdon Sanderson, already referred to (p. 136). He has shown that stimulation of the cone of medullary fibres, which corresponds to a cortical centre, may produce through the corpus striatum the same movement as results from stimulation of the grey matter of the centre itself. That a similar function is performed by the optic thalamus in respect to the sensory centres will be argued subsequently (p. 252). In the optic thalamus and the corpus striatum the association between certain impressions and certain actions becomes so mechanical or organised that, if we were to remove from the dog all the centres above the basal ganglia, these would of themselves, on the application of external stimuli, be sufficient to carry out all the co-ordinated movements of locomotion. We have already seen that in the fish, frog and pigeon the mesencephalic centres alone are capable of such co-ordination. The pigeon without its cerebral hemispheres is not the functional homologue of the dog without its hemispheres, but of the dog still retaining its optic thalami and corpora striata. In such a condition, however, the dog would have no more spontaneity than the pigeon deprived of its hemispheres, and would, like it, be a piece of mechanism, capable of action only in direct response to external stimulation.

The dog from which the cortical motor centres only have been removed, is, however, in a very different position. It retains its sensory centres, and is a conscious, sentient animal, and is capable of ideation and emotion (see Chap. XI.). It is not merely a mechanism the activity of which is dependent purely on external stimulation, but has within itself the springs of action in the mediate form of revived or ideal impressions, and is thus capable of spontaneous action. As, however, the revived impressions occupy the same place, or coincide with the physiological activity of the same parts as are engaged in the consciousness of present impressions (§ 91), the revived impressions can throw the automatic apparatus of movement into action just as well as immediate or present impressions. Examples of this mode of action are frequently seen under the influence of emotion in man. Emotion may get at and excite the automatic centres independently of volition.

In these cases, and in the dog deprived of its cortical centres, the path from impression to action is not, as in the ordinary course of volition, through the cortical motor centres to the corpus striatum, and thence downwards to the motor nuclei and motor nerves, but through the basal ganglia directly.

A dog, therefore, deprived of its cortical motor centres, may yet be capable of spontaneous action and co-ordinated locomotion, under the influence of present or past impressions, or of emotional states. Only such movements, however, will be excited as have been automatically organised in the corpora striata. The movements of locomotion having become automatic, may thus be easily effected, and the dog may be able to walk with as much apparent steadiness as before. Such forms of activity, however, as are not habitual, and have not become automatic, would be rendered impossible. It may be confidently asserted, and perhaps it may be one day resolved by experiment, that any special tricks of movement which a dog may have learnt, would be as effectually paralysed by removal of the cortical centres, as the varied and complex movements of the arm and hand of the monkey by the same lesion. This method of explanation of the apparent recovery of voluntary power in dogs deprived of the cortical motor centres, appears to me much more in harmony with experimental data and with clinical observation, than the hypothesis of direct functional substitution of one centre by another, which, however well it may serve to explain such phenomena in the dog, involves otherwise so many manifest inconsistencies and contradictions.

§ 74. I now pass to the consideration of the views of Nothnagel, Hitzig and Schiff, respecting the function of these cortical regions. Nothnagel is of opinion that the affection of motility from destruction of these centres is due to paralysis of the 'muscular sense' (Muskelsinn). He thinks that the recovery of movement proves that the centre (Endstation) of the muscular sense is not itself destroyed, but that the destruction of the cortical centres has only interrupted the path of centripetal impressions; and thus, that the phenomena are similar to those of locomotor ataxy (Virchow's 'Archiv,' 57, 1873).

Hitzig, in his commentaries on the experiments made by himself and Fritsch, attributed the affection of motility to an imperfect consciousness of the state of the limbs, a condition resembling the ataxy in tabes dorsalis. He believed that there still remained a path of conduction from the 'mind' (Seele) to the muscle, seeing that motion was not entirely paralysed, but that the centripetal path from the muscle to the 'mind' was somehow interrupted. And he concludes: 'Probably this interruption occurred in the endstation of the hypothetical path of the muscular sense (Muskelsinn), at any rate it had its seat in the centre which we had destroyed' (Reichert's u. Dubois-Reymond's 'Archiv,' 1870). In his subsequent experiments (*idem*, 1873, and 'Untersuchungen in das Gehirn,' p. 59), Hitzig fights shy of the term 'muscular sense' (Muskelsinn). And in his latest researches (Reichert's u. Dubois-Reymond's 'Archiv,' 1874), he describes the effect of destruction of the cortical centres as a loss of 'muscle-consciousness' (Muskelbewusstsein).

Schiff ('Archiv für Exp. Pathologie und Pharmacologie,' Bd. iii. 1874, p. 171) is of opinion that the movements of the limbs resulting from stimulation of the cortical centres are of a reflex nature, and that the affection of motility from destruction of these centres is essentially an ataxy dependent on loss of tactile sensibility. In support of this view, he shows that agents which annihilate reflex excitability, also annihilate the excitability of the cortical centres, while motor nerves still continue excitable. I have already replied to this argument (p. 134), and shown that different parts of the nerve centres differ in their degree of excitability under the chloroform narcosis.

To determine whether sensation is excited before the muscular movement results, is a problem incapable of being solved in the lower animals; but the facts of localised convulsions in man from irritation of the cortex completely dispose of this supposition. For it is found that in these cases in which limited convulsions occur, the movements are not preceded or associated with any sensation further than that which accompanies the violent muscular contractions. But the most conclusive proof of the untenability of Schiff's hypothesis, is the fact that sensibility to touch, pain, etc., is absolutely unimpaired after destruction of these centres. No one has ever observed such want of reaction to tactile stimuli as would indicate loss of tactile sensibility, either in man, monkeys or dogs; and the nature of the argument which Schiff employs to establish this loss of tactile sensibility is not one calculated to weigh much against the most positive indications of its retention. Schiff argues, that because animals in which the cortical centres are destroyed, *resemble* in their gait the movements of animals in which the posterior columns of the cord are divided, and because in the latter case the ataxia is due to diminution or abolition of the sense of contact, therefore the cerebral ataxy is due to a similar cause. Mere resemblance, however, is not identity, even though we were to admit the fact of resemblance to the fullest extent. The resemblance utterly fails in the case of the monkey, where there is no ataxy, but complete paralysis, and the phenomena in the dog, which Schiff relies on in support of his view, are clearly due to a condition of paresis of movement not amounting to complete paralysis, a condition which has already been accounted for.

Schiff's hypothesis, therefore, resting as it does mainly on the shallow foundation of a questionable resemblance, and contradicted by such facts as the total paralysis of movement, with retention of tactile sensibility in man and the monkey, and the dependence of tactile sense on a totally different part of the brain (§ 67), is incapable of being maintained.

The views of Nothnagel and Hitzig differ from that of Schiff chiefly in this, that they attribute the affections of motility consequent on destruction of the cortical centres to the loss of muscular instead of tactile sensibility. Nothnagel in particular expressly defines the condition as due to loss of the 'Muskelsinn,' while Hitzig prefers the term loss of 'Muskelbewusstsein.' Of his dogs he says: 'sie hatten offenbar nur ein mangelhaftes Bewusstsein von den Zuständen dieses Gliedes, die Fähigkeit sich vollkommene Vorstellungen über dasselbe zu bilden, war ihnen abhanden gekommen' (Unt. ü. d. Gehirn. p. 60). This muscle-consciousness is composed of several factors, principally, as he says, of our 'perception of the condition of the muscles, and to a less degree of the joints, skin, etc.' (*Op. cit.* p. 61.)

As generally understood, the muscular sense is regarded as dependent on centripetal impressions, derived either from the muscular contraction alone, or from these in combination with coincident impressions arising in the skin, fasciæ, ligaments and joints during the act of muscular contraction. This is the acceptation in which Nothnagel understands the muscular sense, and he regards the cortical centres of the limbs as in some manner directly connected with the paths of these centripetal impressions, so that when these centres are destroyed, affections of motility ensue in consequence of the loss or impairment of the sensations which accompany and guide muscular contraction. Hitzig does not, except in the above quotations, further expressly define the conditions of muscular consciousness, but as he, like Nothnagel, considers the affection of motility to be due to loss or impairment of the muscular sense or consciousness, it is to be concluded that he regards these centres as the seat of this sense.

Loss of the muscular sense, without any affection of the other forms of common or tactile sensibility, is a condition the existence of which is purely hypothetical. Neither Hitzig nor Nothnagel, nor any investigators into this subject, have been able to furnish the slightest evidence of impairment or loss of the common forms of sensibility, either as regards tactile, thermal or painful stimuli, when the cortical centres are destroyed. That the muscular sense only is destroyed has no better foundation than that the tactile sense is abolished. The affection of motility only resembles ataxia in the case of the cat, dog, etc., but in man and the monkey the resemblance fails, for in these there is complete motor paralysis, with distinct retention of the pristine sensibility to the various forms of cutaneous stimulation. The argument from mere resemblance is thus seen to fail when a wider comparison of instances is made. But further, it has been shown that the condition which may with truth be described as loss of muscular sense or of muscle consciousness, is dependent on lesion of a totally different part of the brain, *viz.*, the hippocampal region or centre of tactile consciousness. With the abolition of sensibility to all forms of cutaneous stimuli, a condition of motor paralysis is induced, which, as exemplified also in cases of cerebral hemianæsthesia, is due to the loss of those centripetal impressions which accompany and guide muscular contraction. In this condition the power of movement remains, but there is no consciousness of the position of the limb, or of the state of contraction of the muscles, and unless guided by the eye, the limb is practically a piece of mechanism entirely detached from the domain of consciousness. Of a muscular sense there remains not a vestige. The individual cannot voluntarily direct or estimate the extent of his movements except with the aid of vision ; and when his eyes are shut, he may will a movement and think he has carried it out, when the limb has never been moved, or been checked midway.

§ 75. It is, however, maintained by Bain (' The Senses and the Intellect,' 1864), and by Wundt ('Menschen- u. Thier-Seele,' vol. i., and ' Physiolog. Psychologie,' 1874), that we have a muscular sense, or consciousness of muscular contraction, independently of centripetal impressions originated by the act of muscular contraction itself.

Bain, who was the first to enunciate this doctrine, thus expresses himself : ' As the nerves supplied to the muscles are principally motor nerves, by which the muscular movements are stimulated from the brain and nerve-centres, our safest assumption is *that the sensibility accompanying muscular movement coincides with the outgoing stream of nervous energy, and does not, as in the case of pure sensation, result from an influence passing inwards, by in-going or sensory nerves*' (*op. cit.* 2nd ed. p. 92). According to this hypothesis, the motor centres and motor nerves would be at once the means of effecting muscular contraction, and the means by which the consciousness of muscular effort is generated.

There is, however, no physiological or pathological evidence in support of the theory that the motor nerves are also the path of transmission of the impressions generated by muscular contraction. In those cases, chiefly of ataxia, in which the muscular sense is impaired or abolished, the organic lesions do not invade the motor nerves or motor columns of the spinal cord. Yet, notwithstanding the integrity of the motor tracts, we see a marked affection of the muscular sense. It may, however, be said that in these cases the loss of muscular discrimination is to be ascribed to the absence of those sensations usually associated with muscular contraction, and aiding discrimination, but not forming the essential basis of this special sense. If, however, the total abolition of the various forms of common sensibility in a limb, practically annihilates the muscular sense, we must, on the principle—*entia non sunt multiplicanda*—question the existence of a muscular sense, unless it can be shown that we may have a consciousness of muscular effort independent of the fact and extent of muscular contraction itself. For this is the only condition by which the possibility of centripetal impressions from muscle, skin, ligaments, etc., can be excluded.

That we may have a consciousness of effort under such conditions is supported by many plausible arguments.

Among the facts adduced, however, there are some which count for little. Of this kind are the experiments of W. Arnold (‘Die Verrichtungen der Wurzeln der Rückenmarksnerven,’ Heidelberg, 1844). Arnold cut the posterior roots of the nerves of the frog's leg, and observed that when the animal was made to jump, it used the leg operated on with apparently as much precision and energy as the sound one. From this the conclusion is drawn that the animal must still have retained the consciousness of muscular effort, otherwise it could not have used the limb in the manner described. We know, however, that the precision of the movements of locomotion in a frog is just as great when the cerebral hemispheres are entirely removed, and that bilateral reflex action of the limbs is easily produced in this animal by unilateral cutaneous stimulation. Psychical discrimination, a function which belongs to the hemispheres, forms no essential factor in the co-ordination of the frog's movements of locomotion. Arnold's experiment is nothing more than a very ordinary instance of bilaterally co-ordinated reflex action, and may be demonstrated in a frog deprived of its cerebral hemispheres, and therefore of all truly psychical faculties. To argue from the responsive or reflex actions of the frog to the conditions of psychical discrimination in man, is not, I think, likely to lead to trustworthy conclusions. Certain facts observed in cases of hemiplegia in man, alluded to in the following quotation from Wundt, are more to the point :

'Whether the sensations accompanying the contraction of the muscles arise in the nerve fibres that transmit the motor impulse from the brain to the muscles, or whether special sensory fibres exist in the muscles, cannot be decisively settled. [See, however, p. 52.] Certain facts, however, make the first assumption more probable. If special nerve fibres existed, they must be connected with special central cells, and thus in all probability the central organs for the apprehension of these sensations would be different from those which send out the motor impulse; there would be two independent nerve systems, the one centripetal, the other centrifugal. But in the one, the medium of the sensation, nothing else could be regarded as the stimulus than the changes taking place in the muscle, the contraction, or perhaps the electrical process in nerve and muscle, accompanying the contraction. Now this process is known to keep equal pace with the energy of the muscular contraction; and we must expect that the muscular sensation would constantly increase and decrease with the amount of internal or external work done by the muscle. But this is not the case, for the strength of the sensation is dependent only on the strength of the motive impulse, passing outwards from the centre, which acts on the innervation of the motor nerves.' (Wundt: 'Menschen- u. Thier-Seele,' i. p. 222. Transl. by Bain, *op. cit.* p. 94, note.) Wundt then quotes instances where the patient suffering from muscular paresis, is still capable of feeling that he is putting forth great muscular effort, though the limb is hardly moved. This would seem to show that the consciousness of effort is independent of the muscular contraction itself. To this may be added certain facts which I myself have repeatedly observed in cases of hemiplegia. I have found that patients suffering from complete paralysis due to disease of the corpus striatum, still express themselves as conscious of putting forth great energy when told to move the paralysed limb, though the limb remains absolutely motionless.

Taking the case of paresis first, we find a simple explanation of the seeming great effort, with only slight movement, in the associations organised by former experience. A slow difficult movement being associated in experience with great resistance or the lifting a heavy weight, will naturally suggest to the mind a similar idea, even though no weight is actually raised. Hence the patient, who can only move his limbs slowly and with difficulty, thinks his arm is weighted with lead or some heavy substance.

This objective projection of subjective associations is well exemplified in paresis of the ocular muscles. In cases of paresis of the external rectus the patient is apt to think that objects lie much further outward than is really the case. The length of time required for the contraction of the enfeebled rectus, would in the normal condition coincide with greater excursion, and therefore greater lateral distance of the object, and hence from association this subjective sensation is projected outwards as greater objective distance. This is a pure musculo-optical illusion, and is analogous to the optical illusions of distance caused by the artificial diminution of the object when seen through the large end of the telescope. In the cases, however, where, notwithstanding complete paralysis, the sense of energy put forth is still experienced by the patient, who tries to move his paralysed limb, subjective associations do not explain the phenomena, and there seems at first sight to be a strong case for attributing the consciousness of effort to the conditions of the central motive impulse.

It is necessary, however, to exclude movements altogether before such an explanation can be adopted. Now, though the hemiplegic patient cannot move his paralysed limb though he is conscious of trying hard, yet he will be found to be making powerful muscular exertion of some kind. Vulpian has called attention to the fact, and I have repeatedly verified it, that when a hemiplegic patient is desired to close his paralysed fist, in his endeavours to do so he unconsciously performs this action with the sound one. It is, in fact, almost impossible to exclude such a source of complication, and unless this is taken into account very erroneous conclusions as to the cause of the sense of effort may be drawn. In the fact of muscular contraction and the concomitant centripetal impressions, even though the action is not such as is desired, the conditions of the consciousness of effort exist without our being obliged to regard it as depending on central innervation or outgoing currents.

It is, however, easy to make an experiment of a simple nature, which will satisfactorily account for the sense of effort, even when these unconscious contractions of the other side, such as hemiplegics make, are entirely excluded.

If the reader will extend his right arm and hold his forefinger in the position required for pulling the trigger of a pistol, he may without actually moving his finger, but by simply making believe, experience a consciousness of energy put forth. Here, then, is a clear case of consciousness of energy without actual contraction of the muscles either of the one hand or the other, and without any perceptible bodily strain. If the reader will again perform the experiment, and pay careful attention to the condition of his respiration, he will observe that his consciousness of effort coincides with a fixation of the muscles of his chest, and that in proportion to the amount of energy he feels he is putting forth, he is keeping his glottis closed and actively contracting his respiratory muscles. Let him place his finger as before, and *continue breathing* all the time, and he will find that however much he may direct his attention to his finger, he will experience not the slightest trace of consciousness of effort until he has actually moved the finger itself, and then it is referred locally to the muscles in action. It is only when this essential and ever present respiratory factor is, as it has been, overlooked, that the consciousness of effort can with any degree of plausibility be ascribed to the outgoing current. In the contraction of the respiratory muscles there are the necessary conditions of centripetal impressions, and these are capable of originating the general sense of effort. When these active efforts are withheld, no consciousness of effort ever arises, except in so far as it is conditioned by the local contraction of the group of muscles towards which the attention is directed, or by other muscular contractions called unconsciously into play in the attempt.

I am unable to find a single case of consciousness of effort which is not explicable in one or other of the ways specified. In all instances the consciousness of effort is conditioned by the actual fact of muscular contraction. That it is dependent on centripetal impressions generated by the act of contraction, I have already endeavoured to show. When the paths of the centripetal impressions, or the cerebral centres of the same, are destroyed, there is no vestige of a muscular sense. That the central organs, for the apprehension of the impressions originating from muscular contraction, are different from those which send out the motor impulse, has already been established. But when Wundt argues that this cannot be so, because then the sensation would always keep pace with the energy of muscular contraction, he overlooks the important factor of the fixation of the respiratory muscles, which is the basis of the general sense of effort in all its varying degrees.

In the first instance, our consciousness of the extent and energy of our muscular contractions, and the faculty of muscular discrimination, are derived from the centripetal impressions generated by the contraction itself. The association of the sensory impression with the corresponding movement, however, becomes by education so precise, and the nexus so firmly welded, that we can apparently by intuition estimate the exact degree and extent of movement necessary to accomplish any desired end. It is further possible, by reviving the sensory impression, to recall in idea the movement which coincided with it, even though the muscles themselves, to which the movement is referred, have been severed from the body.

Many remarkable instances of this kind are given by Weir-Mitchell in his able work on 'Injuries of Nerves.'

'If we faradise the track of the nerves in or above the stump, we may cause the lost fingers and thumb to seem to be flexed or extended, and, what is most remarkable, parts of which the man is conscious, but which he has not tried to stir for years, may thus be made to appear to move, to his utter amazement. In one case I thus acted on the nerves so as to cause a thumb, which for years was constantly and violently bent in on the palm, to straighten out completely. On breaking the circuit, without warning, the patient exclaimed that his thumb was cutting the palm again, and the same result was obtained by shifting the conductors, so as to put the nerves out of the circuit. In a case of amputation of the shoulder-joint, in which all consciousness of the limb had long since vanished, I suddenly faradised the brachial plexus, when the patient said at once, "My hand is there again; it is bent all up, and hurts me." These impressions are correctly referred by the patient, so that the faradisation of the musculo-spiral or the ulnar gives sensation of movement in the related parts. It is, of course, impossible that the motor nerves stimulated should convey any impression centrally; and we must conclude that irritation of sensory trunks may occasion impressions of muscular action in the sensorium' (*Op. cit.* p. 359).

The explanation of these curious phenomena is correctly indicated by Weir-Mitchell. The excitation of the sensory nerves calls up in idea the correlated movement, *i.e.* the movement which in the actuality of past experience had coincided with the sensation now revived by the faradic stimulus. This, of itself, is a strong argument in favour of the centripetal origin of the impressions of muscular activity. According to Bain's 'Law of Contiguity,' 'actions, sensations and states of feeling, occurring together or in close succession, tend to grow together, or cohere, in such a way that when any one of them is afterwards presented to the mind, the others are apt to be brought up in idea.' The ideal associated movement is thus made to arise in consciousness, when the corresponding sensation is artificially re-excited. The organic register of sensory impressions is, however, anatomically distinct from that of movements, and it is only by the association of actual experience, that an organic nexus is established between the two. We have a memory of sensations and a memory of movements, organically distinct from each other; but, by association, a memory of sensations combined with movements. Such is the complex memory of acts of musculo-sensory discrimination.

And just as by excitation of the sensory part of the nexus the associated movement is called up in idea, so we may theoretically suppose that the excitation of the motor part will revive in idea the associated sensation. That this in reality occurs, is likewise shown by Weir-Mitchell. 'Persons who have had an arm amputated are frequently able to will a movement of the hand, and apparently to execute it to a greater or less extent.' A small number have entire and painless freedom of motion, as regards all parts of the hand. 'My hand is now open, or it is shut,' they say. 'I touch the thumb with the little finger,' 'The hand is now in the writing position,' etc. Between these cases and such as are conscious of an immobile member, every grade of difference as to motion is to be found, with equally wide varieties as to the associated pain, which, perhaps, is most acute in such as will with vigour a motion that they seem to fail of executing' (p. 357).

In some of these cases the muscles which move the hand remain, and, therefore, as the possibility of centripetal impressions remains, such cases must be excluded. 'In others, as in shoulder-joint cases, or amputations through the humerus, the muscles which act on the hand are absent altogether; yet in these there is fully as clear and definite a consciousness of the movement of the fingers, and of their change of positions, as in the former cases.' Weir-Mitchell is of opinion that these facts tend to support the view which Bain maintains, that in the very act of volition, apart from sensory experience, the amount and extent of movement is at once given. A similar opinion is expressed by Hughlings-Jackson (leading article, 'Brit. Med. Jour.,' Oct. 9, 1875). The case, however, is clearly parallel to the revival of movement in idea, when the sensation is presented. Here the movement is willed, and the corresponding sensation, as to the position and state of the fingers, is called up in idea. This is, however, only a revival of past experiences, which is a very different thing from present acts of muscular discrimination. There is no more reason why we should not be able to revive in idea past movements, and the associated sensations, when the limb by which the experience was gained is amputated, than recall visual impressions after extirpation of the eyeballs. But, as we cannot any longer see when the eyes are destroyed, so we can no longer exercise muscular discrimination, or gain musculo-sensory experience, when the limbs are amputated. We retain what we have already acquired, but make no further advance. But, whether we make the movements in reality, or revive them in idea, the consciousness of the extent and energy of the movements is, in my opinion, in all cases dependent on in-going or centripetal impressions. In the case of actual movements, the impressions arise directly in the periphery; in the case of ideal movements, the sensory impressions arise by associated excitation of the centres which form the organic register of impressions primarily originating in the periphery (see Chap. XI).

The centres of centrifugal, or motor, impulses are anatomically distinct from those of centripetal, or sensory, impressions. The one may be destroyed, while the other remains intact.

The cortical centres, for the movements of the limbs, are concerned purely with centrifugal impulses, and are clearly differentiated from the paths and terminal centres of the centripetal impressions on which muscular discrimination is based.

The destruction of the centripetal centres abolishes muscular sense, or muscle consciousness, though the power of movement remains. The destruction of the centrifugal centres abolishes the power of voluntary motion, and, therefore, prevents the exercise of muscular discrimination, but the transmission and perception of centripetal impressions continue unimpaired.

§ 76. It would be a crucial test of the dependence of the muscular sense on centripetal impressions, if it could be shown without fallacy, that muscular discrimination can still be exercised, when the muscles are made to contract artificially by means of the electric stimulus. Experiments on this point have been made by Bernhardt ('Archiv für Psychiatrie,' vol. iii. 1872, p. 618); but, owing to the difficulty of excluding the sense of cutaneous pressure, he came to no positive conclusions. Though Bernhardt himself is inclined to regard the muscular sense as a 'Function der Seele,' only aided by centripetal impressions, his experiments show that differentiation of weights can be made when the muscles are excited to contraction by the electric current alone.

'Gesunde Menschen unterscheiden in dieser Feinheit aber auch, wenn die Beugung des Fingers, und damit das Heben der Gewichte durch die electrischen Strom bedingt war.'

According to the law of perception of weight by the sense of cutaneous pressure alone, it requires the addition of one-third of the original weight, whatever it may be, to produce a distinctly perceptible difference. But in Bernhardt's experiments on the foot, it was found that the addition of from 3 to 5 Loth ($1\frac{1}{2}$ to $2\frac{1}{2}$ oz.) to an original weight of from a pound to a pound and a half, could be distinctly perceived, which is less than one-half the increment perceptible by cutaneous pressure alone.

In regard to the discrimination of weight by the finger, the sensibility was found to be much finer. Three drachms could be distinctly differentiated from nothing, and to heavy weights (say 1 lb.) the addition of 5 drachms was distinctly perceived, *i.e.*, a difference of about $\frac{1}{16}$, a power of discrimination which corresponds pretty nearly with that of the muscular sense, which is capable of detecting an addition of $\frac{1}{17}$th of the original weight. These results, therefore, indicate that the discrimination was much finer than could be effected by the sense of pressure alone, and that, therefore, it depended on muscular discrimination.

Experiments made in reference to this point by myself, with the assistance of Dr. Lauder-Brunton, gave such results as clearly to indicate the retention of muscular discrimination, when the muscles were excited to contract by the galvanic current. The method I adopted was to determine, blindfolded, in the first instance, the differences in weight which could be discriminated by my hand held flat on a cushion, and then to test the muscular discrimination of the same weight, when the wrist was flexed so as to raise the weight with the fingers. By repeated experiments with weights varying from one to six ounces, the average discrimination by the sense of cutaneous pressure was found to be about one-third, while the muscular discrimination accorded pretty nearly with the 1-17th, as usually found to be the rule.

The same experiments were then made with the same hand as regards cutaneous pressure, and by galvanic excitation of the flexor muscles of the hand, so applied as to cause repeated raising of the weight by the fingers. Again the sense of pressure averaged the normal, and again muscular discrimination was found to be almost as accurate as in the former experiments, when the raising of the fingers depended on voluntary effort.

Cutaneous pressure being thus allowed for in both cases, the muscular discrimination by means of the centripetal impressions generated by muscular contraction alone, not depending on voluntary motor impulse, is clearly established.

It is also a very important fact, noted by Leyden (Virchow's 'Archiv,' xlvii.) that ataxic patients, who are said to retain muscular discrimination notwithstanding the abolition of cutaneous sensibility, are not able to discriminate weights until they reach a considerable amount. It is supposed that this is due only to a diminution, owing to the absence of the usually associated sensations of pressure. But I am of opinion that the discrimination of heavy weights calls into play the general sense of effort which, as we have seen, is to be more properly ascribed to the region of the respiratory muscles; and that the discrimination in this case is effected by the amount of bodily strain and fixation of the muscles of the chest, necessary to support a heavy weight; and that it is not a question of the muscular sense of the limb at all, unless this is absolutely eliminated by continuous and easy respiration during the trial. When this is eliminated it will be found that the sense of local resistance is the only element in the discrimination of weight.

§ 77. Among the reactions excited by electrisation of the anterior or motor part of the hemispheres, is one of a special character, *viz.*, that which results from stimulation of (12) in the monkey, and the corresponding point in the brain of the dog and jackal. The head and eyes are directed to the opposite side, and at the same time the pupils dilate widely. In the jackal, moreover, the head assumes the position which is characteristic of fixed attention. In the monkey the attitude is also one of excited attention or surprise. That this centre is the one concerned in those movements expressive of attentive observation, is extremely probable. It is to the associated action of this centre that I attribute the greater part of the motor reaction, on stimulation of the superior temporo-sphenoidal convolution in the monkey. In addition to the sudden retraction of the ear, the special reflex sign of excitation of subjective auditory sensations, the animal almost constantly turned its head and eyes to the opposite side, a movement which indicated the sudden direction of the attention to the source of the sound. Similar movements, but not in all cases, were induced also in cats, dogs, etc., by stimulation of various sensory centres when the reaction was active, and such as would coincide with greater receptivity, and greater attentiveness to sensory impressions. These, though aroused subjectively, would naturally be referred by the animal to external sources, and the attention would be directed accordingly.

What the effect of conjoint and equal stimulation of the corresponding centres in both hemispheres may be, has not been determined experimentally. *A priori*, however, we should not expect convergence of the eyes, but rather a fixation of the eyes and dilatation of the pupils in the position of accommodation for distance. The two eyes are naturally associated together, the one turning outwards and the other inwards. From the cross action of the hemispheres, however, the outward movement, or the one to the opposite side, must be regarded as the primary. This is further justified by the lateral deviation of the eyes which is observable in cases of hemiplegia in man. In right hemiplegia from hæmorrhage into the left hemisphere, the head and eyes at first deviate to the left, or the sound side. This is clearly due to the action of the motor centre in the right hemisphere, which, no longer counterbalanced by the corresponding centre in the left, causes deviation of the head and eyes to the left side.

The motor function of this centre is thus clearly established, active movement resulting from its stimulation, and paralysis resulting from its destruction. The paralysis is transient, but this is explicable on the principle already enunciated, that associated movements are rarely permanently or totally paralysed.

The Antero-Frontal Regions of the Brain.

§ 78. Electrical irritation of the regions in advance and below (12) in the brain of the monkey, was in general attended by negative results. This negative region also includes the island of Reil, which may be considered the starting point of the frontal convolutions. So likewise in the cat and dog, the regions in advance of the anterior limb of the sigmoid gyrus may be regarded as yielding no outward results, such phenomena as occur being irregular in character, and without doubt due to conduction of currents to the neighbouring parts.

The only exception to the negative results of stimulation of the antero-frontal regions which I have observed in the case of the monkey, was that in one animal the stimulation of these regions caused movements of the eyeballs. These were not constant in character, the eyes being sometimes moved laterally, sometimes upwards. No dilatation of the pupils was produced.

These effects may have been only coincidences. Removal or destruction by the cautery of the antero-frontal lobes is not followed by any definite physiological results. The animals retain their appetites and instincts, and are capable of exhibiting emotional feeling. The sensory faculties, sight, hearing, touch, taste and smell, remain unimpaired. The powers of voluntary motion are retained in their integrity, and there is little to indicate the presence of such an extensive lesion, or removal of so large a part of the brain. I have removed the frontal lobes as indicated by the line *a b* (fig. 55), almost completely in three monkeys, with the same negative results, and what is more remarkable, I found that the removal of these lobes in an animal which had recovered from ablation of the occipital lobes, caused no symptoms indicative of affection or impairment of the special sensory or motor faculties.

FIG. 55.—The Brain of the Monkey. *a b* indicates the line of section for removal of the frontal lobes.

And yet, notwithstanding this apparent absence of physiological symptoms, I could perceive a very decided alteration in the animal's character and behaviour, though it is difficult to state in precise terms the nature of the change. The animals operated on were selected on account of their intelligent character. After the operation, though they might seem to one who had not compared their present with their past, fairly up to the average of monkey intelligence, they had undergone a considerable psychological alteration. Instead of, as before, being actively interested in their surroundings, and curiously prying into all that came within the field of their observation, they remained apathetic, or dull, or dozed off to sleep, responding only to the sensations or impressions of the moment, or varying their listlessness with restless and purposeless wanderings to and fro. While not actually deprived of intelligence, they had lost, to all appearance, the faculty of attentive and intelligent observation. It might be supposed that such a serious lesion would cause an amount of constitutional disturbance and fever, sufficient to account for the languor and disinclination to active exertion ; but this is not consistent with the fact that they continued to eat and drink heartily, and to exhibit no signs of physical prostration, when the mood to wander about was upon them. In fact, after such operations constitutional disturbance only begins to manifest itself, when, as is usually the case, encephalitis sets in, but this rarely occurs within twenty-four hours, and may not exhibit itself to any extent for several days, during which ample time is allowed for careful observation and the application of various tests of the animal's faculties, powers and behaviour.

What the physiological function of the frontal lobes may be is, therefore, not clearly indicated, either by the method of excitation or by the method of destruction. That the removal of the frontal part of the hemispheres in dogs causes no positive symptoms, in the domain of sensation or voluntary motion, is also proved by the experiments of Hitzig. And that extensive disease may occur in the frontal lobes in man, without any manifest symptoms during life, is likewise illustrated by numerous pathological cases, among which may be reckoned the celebrated 'American crow-bar case' already alluded to (p. 126).

The anatomical relations of the frontal lobes are such as to indicate connection especially with motor ganglia and motor tracts. The basis of the corpus striatum is directed towards the frontal aspect of the hemispheres, and the great mass of the fibres of the *corona radiata*, which radiate from the corpus striatum, are seen to have their cortical distribution especially in the frontal regions.

The motor signification of these parts is indicated therefore by anatomical investigation, but, nevertheless, electrical irritation fails to excite motion, and destruction causes no motor paralysis. What relation these regions have to the function of movement is therefore obscure, and until further light is thrown upon it experimentally, the explanation of this relation must remain more or less hypothetical. As the phenomena consequent on destruction of this region partake more of a psychological than physiological character, further consideration of the functions of the frontal lobes is reserved until the subjective or psychological aspect of brain function is under discussion (Chap. XI.).

Note to Chapter IX.

Since this chapter was written, I have become aware of certain remarkable views advanced by Dr. Brown-Sequard in the Société de Biologie (vide 'Gazette des Hospitaux,' January 1876), and published also in the 'Lancet' of January 1, 15 and 29, for 1876.

Brown-Sequard thinks the cross action of the cerebral hemispheres is an untenable doctrine, and regards each hemisphere as sufficient for the innervation of both sides of the body. He professes to have collected from various sources, ancient and modern, two hundred cases of hemiplegia arising from disease on the same side of the brain.

The paralysis from brain disease, he attributes, not as is usually held, to loss of function in the part diseased, but to an inhibitory influence on centres of motion, excited by irritation starting from the seat of disease or its neighbourhood. As examples of such irritative and inhibitory lesions, all kinds of pathological processes are marshalled, such as tumours, hæmorrhages, abscesses, softenings, etc., indefinite as to position, duration or extent; and also the effects of cauterisation of the cortex cerebri in guinea-pigs, cats, etc.

I have little to add in the way of comment on these views, beyond the various facts and arguments adduced in the above chapter.

Out of the heterogeneous mass of cases collected by Brown-Sequard, not one, to my mind, satisfies the requirements of scientific evidence in a question of this kind.

Even, however, if we admit every one of them, the logical deduction from such facts, taken by the side of the hundreds of thousands of cases of cross paralysis, would be, not that the doctrine of the cross action of the cerebral hemispheres is untenable, but that there may be exceptions, just as there are exceptions to the rule that the heart is situated to the left and the liver to the right. To go beyond this is simply to stultify every well-established rule in the clinical diagnosis of brain lesions; rules which are not the product of preconceived notions, but founded on the irrefragable evidence of unquestioned facts.

As to Brown-Sequard's experimental instances of direct paralysis from cauterisation of the cortex cerebri on the same side, as I have never met with such results, but invariably the reverse, though I have performed numerous experiments of the kind on various animals, I attempt no explanation. On what experimental grounds the cauterisation of the grey matter of the cortex is regarded as an irritant, I fail to discover. I find that destruction of the grey matter by the cautery produces precisely the same effects as excision of the part by the scalpel. Furthermore, I have found that the introduction of the cautery into the lenticular nucleus of the corpus striatum, the motor functions of which I imagine Brown-Sequard admits, causes paralysis of motion on the opposite side of the body without any antecedent excitation, which would necessarily ensue if the cautery really acted as an irritant. The experiments above detailed on the sensory and motor regions of the hemispheres, as well as the facts of clinical observation in reference to unilateral and localised convulsive phenomena from brain lesion, render the differentiation of irritative from destructive lesions a matter of comparative ease and certainty.

More recently Goltz (Pflüger's 'Archiv für Physiologie,' Bd. xiii.) has published the results of an investigation into the effects of destruction of the cortex cerebri in dogs. He removed the grey matter by means of a forcible jet of water directed against the surface,—a method which he thinks preferable to excision or cauterisation, as being less likely to cause profuse hæmorrhage or subsequent inflammation. He finds that when large tracts of the grey matter are thus destroyed, paralysis of tactile sensation, vision and motion occur on the opposite side of the body. These symptoms he thinks are determined more by the extent than by the locality of the lesion. The effects of destruction of the cortex are of two kinds—transient and permanent. The former, *viz.*, complete paralysis on the opposite side, he attributes to irritative inhibition of deep-seated centres; the latter, which he calls 'phenomena of deficiency' (Ausfallerscheinungen), and indicated by a defective interpretation and intelligent use on the part of the animal of its sensory experience and motor powers, he regards as the direct results of the lesion in question. Goltz is evidently unacquainted with the results of my researches on the brain of monkeys, recorded in the above chapter, which were published in abstract early in 1875 ('Proc. Roy. Soc.,' 162), and which define the respective sensory and motor centres, and satisfactorily account for the phenomena he describes. As I have already discussed above the chief questions raised by Goltz, I do not deem it necessary to enter into further and special examination of his views.

CHAPTER X.

FUNCTIONS OF THE BASAL GANGLIA.

§ 79. THE basal ganglia—the *corpora striata* and *optic thalami*—are ganglionic masses, intercalated in the course of the projection system of fibres which connect the cortex with the *crura cerebri*, and through these with the periphery. The corpora striata are the 'ganglia of interruption' of the projection system of the foot or basis of the crus, an anatomical indication of their motor signification.

The ganglionic substance clusters round the peduncular expansion in the form of two great masses, the one of which, projecting into the cavity of the lateral ventricle, receives the name of the *nucleus caudatus*, or intra-ventricular nucleus (fig. 49, S S); the other, situated externally in immediate proximity to the island of Reil, receives the name of the *lenticular ganglion*, or extra-ventricular nucleus of the corpus striatum (fig. 49, L). What exact relation the ganglionic cells have to the peduncular fibres which connect the cortex with the crus, is difficult to determine with certainty, but that they are integrally connected may be regarded as absolutely established.

It does not seem to me possible to differentiate between the peduncular fibres and the ganglionic substance, and they ought to be regarded as a complex whole. For, though we may be able, experimentally, to determine the functions of the cortical centres and of the medullary fibres between them and the corpus striatum, it is impossible to differentiate experimentally between the ganglionic centres and fibres and those, if any, which only pass through to the crus cerebri. Whether the various ganglionic masses of which the corpus striatum is composed have special relations to the individual cortical centres, is a question which I doubt the competence of mere anatomical investigation to resolve; and therefore I shall employ the term corpus striatum to signify generally the ganglionic substance and the fibres, without attempt at differentiation, which converge from it to the crus.

§ 80. The *optic thalamus* bears the same relation to the *tegmentum*, or sensory tracts of the crus cerebri, which the corpus striatum has to the foot or motor tracts. The medullary fibres, which converge to or diverge from the optic thalamus, are apparently distributed in the posterior and temporo-sphenoidal regions of the hemisphere. Various separate ganglionic masses have been described by Luys as constituting the body of this ganglion, under the names of the (1) *centre antérieur*, (2) *centre moyen*, (3) *centre médian*, (4) *centre postérieur*, in connection with the olfactory, optic, tactile and auditory tracts respectively, and with corresponding regions in the cortex cerebri.

However probable this arrangement may be, I hesitate to accept it on the grounds of anatomical investigation alone, especially as the researches of Meynert lead him to different conclusions from those arrived at by Luys.

§ 81. Electrical stimulation of the *corpora striata* in monkeys, cats, dogs, etc. (Chap. VIII. § 63), causes unilateral tonic contraction of the muscles of the face, neck, trunk and limbs, a condition of pleurosthotonus in which the body is bent to the opposite side, and the limbs maintained in a position indicating the predominance of the flexor over the extensor muscles. There is no differentiation of effects as from stimulation of individual cortical centres, but a general unilateral contraction. This result has been confirmed by the experiments of Carville and Duret.

Destructive lesions of the corpus striatum in man produce hemiplegia of the opposite side, sensation remaining unimpaired.

This is regarded as one of the best established facts in human cerebral pathology. It is fully confirmed by destructive lesions of the corpus striatum in dogs and other animals. The effects of excitation, taken with the results of destruction of the corpus striatum, demonstrate, therefore, beyond all doubt, that the corpus striatum has a purely motor signification. The anatomical relations of the corpus striatum with the motor tracts of the crus cerebri are thus verified by physiology and human pathology.

§ 82. The signification of the *optic thalami* is a subject on which there is considerable diversity of opinion, the facts of pathology not being of the same constancy and uniformity as are observable in similar diseases of the corpora striata. Paralysis of motion has been found to co-exist with lesions in the optic thalamus, or conjointly in the optic thalamus and corpus striatum; but the question in dispute is whether lesions of the optic thalamus also cause impairment or loss of sensation. Numerous cases are on record (See collected cases by Luys, 'Recherches sur le Système Nerveux,' 1865, p. 538 *et seq.*, Crichton-Browne 'West Riding Asylum Reports,' vol. v., 1876, p. 227), in which lesions of the optic thalamus have been associated with diminution or abolition of sensation in one or other form on the opposite side of the body; while, on the other hand, many cases have also been reported, in which disease of the optic thalamus has not been associated with similar affection of sensation.

Vulpian has seen only paralysis of motility from lesions of the optic thalamus, but he carefully avoids founding any conclusions on these facts as to the true functional signification of this ganglion: 'Nous ne savons rien des fonctions spéciales des couches optiques' (Leçons, etc., p. 659).

The facts of human pathology being thus uncertain and apparently contradictory, and the views founded on these facts diametrically opposed to each other, we turn to experimental physiology. Here, also, the facts are differently interpreted by different investigators.

I shall first consider this question in the light of my own investigations, and afterwards discuss some of the more recent views, which are opposed to those to which my experiments have led me.

It has been shown that electrical irritation of the optic thalami causes no motor manifestations. This is of itself sufficient to dispose at once of the views of those who would attribute motor functions to these ganglia. The fact that lesions of the optic thalami cause paralysis of motion proves nothing regarding the real functional significance of these ganglia.

The effect of destruction of the optic thalamus in the monkey is illustrated by the following experiment :—

The left hemisphere of a monkey was exposed by trephining in the region of the bridging convolution between the angular gyrus and the occipital lobe. Through the anterior extremity of this gyrus a trocar and canula of small size were introduced in a horizontal direction, so as to traverse the optic thalamus. On withdrawal of the trocar, a stilette with expanding wings was inserted and rotated after the manner employed by Nothnagel (p. 246), so as to break up the tissue with which it should come in contact.

On recovery from chloroform narcosis the animal exhibited little symptom of impairment of sensation on the opposite side of the body, with the exception of some degree of hesitation and caution in the movements of the right limbs. It used the left hands only for purposes of prehension, but reaction to tactile and thermal stimuli continued.

Little or no alteration of this condition was observed twenty hours after the operation. Having reason to believe from accurate measurements that the stilette had not quite penetrated the optic thalamus, I again chloroformed the animal and inserted a wire cautery in the track of the canula, carefully calculating the distance by experiments on the dead brain, so as to traverse the optic thalamus completely.

Before the animal recovered consciousness, the left eye was securely closed. When the animal recovered from narcosis and opened its right eye, the right pupil was found to be dilated. In attempts at locomotion the left limbs alone were used, the right remaining motionless. Active reaction ensued on the application of a hot iron to the left side, but no reaction followed its application to any part of the right side, hand, foot or cheek. The animal moved about by the aid of the left limbs only, turning towards the right side and dragging its right limbs. It was evidently blind, as it made no attempt to avoid obstacles placed in its path until it knocked its head against them. When the bandage was removed from the left eye, the movements became more free, and obstacles were now avoided carefully. The direction of movement was now from right to left principally. Absolute want of reaction to cutaneous stimuli on the right side still continued.

It was observed that though the animal made no use of its right limbs for purposes of prehension or progression, yet in attempting to get up when laid on its back it struggled with all four limbs freely. In other respects the animal seemed perfectly well, eating and drinking heartily. When the condition as to cutaneous sensibility had been again clearly established, the animal was chloroformed to death. On *post-mortem* examination it was found that there was a slight hernial protrusion of the brain substance of the size of a shilling, corresponding to the opening made by the crown of the trephine, and occupying chiefly the upper part of the superior temporo-sphenoidal convolution (see fig. 56). In the centre of this was an opening leading into the optic thalamus.

Fig. 56.—The shading indicates the superficial extent of the lesion in the left hemisphere in the operation for destruction of the optic thalamus. The darker centre indicates the sinus leading into the optic thalamus. Lesion causing right hemianæsthesia.

This had been completely traversed by the cautery almost in the centre of the ganglion, a line or two below the ventricular surface, so that the anterior and posterior extremities of the optic thalamus were separated from each other by a track of softening and disintegration. The cautery had just crossed the third ventricle, and touched the third-ventricular surface of the right thalamus.

As had been conjectured, the expanding stilette had not penetrated the optic thalamus, but had broken up the medullary substance to a considerable extent just external to the ganglion. This was clearly indicated by the irregular laceration and discoloration, easily distinguishable from the track of the cautery. The rest of the brain had a normal appearance.

It is of course to be noted that the lesion of the optic thalamus was not the only condition here. The medullary substance external to this ganglion was likewise injured, and there was moreover some affection of the cortical substance of the hemisphere, in the neighbourhood of the centres of sight and hearing.

It is therefore a question, how much the affection of sight in this case was due to the cortical lesion and to the laceration of the medullary fibres, apart from the optic thalamus lesion.

The chief point on which I wished to satisfy myself, and towards which attention was principally directed, was the condition as to tactile sensation. This, though apparently diminished by the lesion which had caused laceration of the medullary fibres external to the optic thalamus, was not thoroughly abolished until the optic thalamus had been disorganised.

Without for the present attempting to estimate how much was here due to the lesion of the optic thalamus as such, and how much to the medullary lesion external to it, we have in this experiment a conclusive proof of the abolition of cutaneous sensation by an injury in and around the optic thalamus.

It has already been shown that sensation is a function of the cortical centres. The regions of special sensation in the brain of the monkey have already been differentiated by the experiments recorded in Chap. IX.

These experiments are fully confirmed by those of Veyssière (p. 182), in which it was shown that section of the posterior part of the peduncular expansion or internal capsule, external to the optic thalamus, causes hemianæsthesia of the opposite side of the body in dogs. More conclusively as regards the consciousness of sensory impressions, it has been shown that hemianæsthesia occurs in man when the corresponding regions of the peduncular expansion are destroyed by disease, as in the cases reported by Türck, Charcot, Demeaux, Bourneville and others.

In these cases, as has already been observed, we have to deal merely with interruption of the centripetal paths from the organs of sense to the centres of sensation in the hemispheres which have been individually differentiated. These experimental facts and pathological data demonstrate that there is a differentiation of the paths and centres of sensation from the paths and centres of motor impulses. It has also been shown that in the corpus striatum and the anterior part of the internal capsule, the motor paths have been completely differentiated from those of sensation, for destruction of the corpus striatum or of the corresponding peduncular fibres causes loss of voluntary motion, without impairing sensation in the slightest degree. The cortical centres of these tracts have also been localised, and it has been shown that loss of voluntary motion without loss of sensation results from their destruction.

The only path remaining for the transmission of sensory impressions from the periphery to the hemisphere is through the *tegmentum cruris cerebri*, the optic thalamus, and its medullary connections with the cortex. With the exception of the olfactory tract, there is no other medium of connection between the hemispheres and the organs of sense but the one specified.

To assert in the face of these facts that sensation can still continue, notwithstanding the total destruction of the optic thalami, both cells and medullary fibres, is to assert nothing less than a physical impossibility. The phenomena will, however, materially depend on the extent of lesion of the optic thalamus, and in this we have, I think, the key to the explanation of the differences in the clinical symptoms of disease of this ganglion.

The optic thalamus is situated at a point where the sensory and motor tracts of the crus cerebri have not as yet become clearly separated and differentiated from each other. In the corpus striatum and in the anterior part of the internal capsule, the differentiation of the motor from the sensory tracts has become completed, but in the region of the optic thalamus the two are more or less bound up together.

Both experimental investigation and the facts of disease of the spinal cord, have shown that it is much more difficult to interrupt the paths of centripetal impressions than those of centrifugal or motor impulses. A much more complete disorganisation of the sensory paths is necessary in order that sensation be entirely abolished. The same law seems to hold good in the case of the optic thalamus. A lesion extensive enough to cause interruption of the not as yet completely separated motor paths, may cause hemiplegia without loss of sensation. Loss of sensation only follows complete disintegration, and in such cases only will hemianæsthesia result along with hemiplegia. The recorded instances, therefore, of so-called destruction of the optic thalamus without loss of sensation, must be put down as only partial lesions, and unless more satisfactory evidence is brought than the mere naked-eye appearances of the optic thalamus in such cases, they cannot for a moment be placed against the positive cases, now numerous, in which loss of sensation has been demonstrated to result from lesions situated in this ganglion.

§ 83. If the optic thalamus is the centre of convergence or ‘ganglion of interruption’ of the sensory tracts of the projection system, we should expect affections of the other senses besides tactile sensation to result from lesion of this ganglion. A close approximation to this result is furnished by the effect of lesions of the internal capsule external to the optic thalamus. Coincident with this lesion, impairment or abolition not merely of tactile sensibility, but also of sight, hearing, taste and smell on the opposite side, have been observed in man. The cause of affection of the sense of smell in the opposite nostril has already been discussed (p. 191). Complete disintegration of the optic thalamus ought to produce similar results. On this point, however, there is need of further careful experimental as well as clinical observation.

In the experiment on the monkey above recorded (p. 239) the conditions of tactile sensibility and sight were alone investigated. As to the unilateral blindness in this case there could be no doubt; but the conditions of experiment were such as to complicate the direct lesion of the thalamus with lesion of the medullary fibres, and to introduce difficulties in the estimation of the effects due to each.

That the blindness in this case depended, however, mainly on the optic thalamus lesion appeared to me indicated by the dilatation of the pupil, a condition which I have not observed to result from destruction of the angular gyrus. Dilatation of the pupil has not been observed in those cases of cerebral hemianæsthesia in man, where the lesion is in the medullary fibres.

The records of human pathology are not in all respects satisfactory or complete. Luys has collected a number of cases of disease of the optic thalamus, in which affections of sight and hearing have been observed in addition to affections of tactile sensation, but the cases described are not all of such a nature as to satisfy the requirements of scientific evidence. Thus many of them were tumours. Conclusions as to the specific effect of such lesions are to be received with the utmost caution.

Apart, however, from tumours, there are lesions which more or less bear out the views which Luys has always so firmly maintained respecting the sensory signification of the optic thalamus. (See Luys' 'Recherches sur le Système Nerveux.') Among more recent and carefully observed cases there is one by Hughlings-Jackson which presents certain features of extreme interest and value. ('A Physician's Notes on Ophthalmology,' 2nd Series, p. 11. Reprinted from the London Hospital Reports, vol. viii. part 2, 1875.) This is a case in which *post mortem* it was found that 'the right optic thalamus presented a considerable depression over its posterior half, where it was much softer than that of the opposite side. On section the tissue was seen to be softened, greyish yellow in tint. The amount of softening was greatest on the inner side, the posterior tubercle (pulvinar) being broken down and destroyed, and here the softening extended up to the ventricular surface. It did not extend beyond the limits of the thalamus into the white substance of the hemisphere or the crus, and the anterior half of the thalamus and posterior extremity of the corpus striatum were intact.' There was no disease in any other part of the brain. Here we have a clear uncomplicated case of lesion of the optic thalamus, and the symptoms observed are manifestly to be attributed to this lesion. The symptoms observed were, feebleness of movement on the left side, particularly in the leg, great diminution of tactile sensation on the left side, impairment of smell, or at least of common sensibility in the left nostril, doubtful diminution of taste on the left side of the tongue, doubtful diminution of hearing in the left ear, and, which is one of the most interesting features of the case, left hemiopia of both eyes owing to paralysis of the right side of both retinæ. This case, though not in all respects absolutely conclusive, owing to the lesion being limited, strongly corroborates the view arrived at on other grounds, that the optic thalamus contains the sensory paths of all the nerves of sensation which take origin below the crura cerebri. The hemiopia is a fact of special importance, and argues strongly in favour of the views of Charcot, in respect to the mode in which retinal impressions reach the cerebral visual centres. As has been already described (p. 168, fig. 45), the corpora geniculata contain fibres from both retinæ, *viz.*, from the inner side of the opposite eye, and from the outer side of the eye on the same side. These latter, however, pass on to the corpora quadrigemina, where they decussate with their fellows, and ascend to the opposite hemisphere. The corpora geniculata of the right optic thalamus contain therefore fibres coming from the right side of both retinæ. Hence, as in this case, lesions of the right corpora geniculata, or of the posterior part of the right optic thalamus, interrupt the path of both sets of impressions, and produce left hemiopia by paralysing the right side of both retinæ. The angular gyrus of the right hemisphere, however, is in relation with the opposite eye alone, receiving the fibres of the right corpora geniculata directly, *i.e.* the fibres from the right side of the opposite eye, and the fibres of the left side, after they have decussated in the corpora quadrigemina. This is proved by the fact that destruction of the angular gyrus in the monkey causes complete loss of vision in the opposite eye, and by the fact that in cerebral hemianæsthesia from lesion of the posterior part of the internal capsule, vision is affected only on the opposite side. Hence, it is obvious that the paths have united in their transit on towards the cortical centre; and that this union takes place in their course through the optic thalamus is borne out by the experiment above recorded, where loss of vision in the opposite eye resulted from a lesion of the optic thalamus occupying the centre of this ganglion. It seems probable, therefore, that the effects of lesions of the optic thalamus upon vision will vary according to the exact position of the lesion. We should expect hemiopia of both eyes from a lesion occupying the region of the corpora geniculata; total unilateral blindness in the opposite eye if the lesion is central; and if the lesion is very extensive, perhaps total loss of vision in the opposite eye, and nasal hemiopia on the same side.

In experiments on the lower animals, as has already been remarked, the determination of partial affections of vision is extremely difficult. The decisive settlement of such points must depend mainly on careful clinical and pathological research.

It appears to me that the various anatomical and physiological considerations which have been advanced establish conclusively that the optic thalamus contains the paths of sensation, and that where the facts of pathology do not seem to bear out this view, an explanation can be given of the absence of sensory affection, consistently with experimental and pathological data; while, to found on negative instances the view that the optic thalamus is not specially related to the sensory tracts, would involve physiological and anatomical impossibilities, and diametric contradiction of well-established positive cases.

§ 84. The above considerations have been founded mainly on the results of clinical and pathological research in man, and experimentation on monkeys.

Experiments on rabbits, dogs and other animals have led to different views respecting the signification of the optic thalami in different hands.

Fournié (‘Recherches Expérimentales sur le fonctionnement du Cerveau,’ 1873) caused destructive lesions of the optic thalami by the injection of a strong solution of chloride of zinc into their substance. Fournié found that destruction of the optic thalami in this way caused loss of sensation. His method, however, is open to serious objection. Owing to the diffusion of the caustic solution to other regions than those in which it is desired to localise the action, such complex results ensue as to render conclusions from them extremely doubtful.

Nothnagel (Virchow's ‘Archiv,’ lxii. 1874), who at first followed a similar method, *viz.* the injection of chromic acid, abandoned it in his experiments on the optic thalami, on account of diffusion. He adopted the method of breaking up these ganglia by means of a canula and trocar with expanding wings, which could be opened out and rotated, when inserted to the proper depth. By this method he professes to be able to cause complete and localised destruction of the basal ganglia.

Nothnagel, from such experiments, states that destruction of the optic thalami in rabbits causes paralysis neither of sensation nor of motion. There appears to be no distortion of the limbs or trunk, and the animals react to cutaneous stimulation as before, springing when the tail or extremities are pinched, and making to sensory stimulation in general the usual outward reactions.

Even when the lenticular nuclei of the corpora striata were destroyed, along with the optic thalami, the animals still continued to react to cutaneous stimulation, and spring when pinched, retaining the power of co-ordinated progression, but not capable of carrying out these movements voluntarily. Now, if these phenomena, especially the combined results of destruction of both basal ganglia, be compared with the results of complete removal of the cerebral hemispheres, it is difficult to discover what Nothnagel has added to the facts already carefully and accurately determined by the experiments of Flourens, Longet and Vulpian, etc. Practically, Nothnagel's destruction of both basal ganglia is equivalent (though, to my mind, a less satisfactory method of operation) to complete removal of the cerebral hemispheres. If sensation can continue after removal of the cerebral hemispheres, and if the reactions to cutaneous and other forms of sensory stimuli exhibited by animals deprived of their cerebral hemispheres, are proofs of sensation or consciousness of sensory impressions, then we may admit that the phenomena described by Nothnagel indicate that sensation is not abolished by destruction of the optic thalami. But it seems to me surprising that this investigator should have so utterly ignored the very point in dispute, and settled to his own satisfaction, so easily, without adding a single new fact to those already clearly ascertained by former experimenters, a question of such importance in cerebral physiology. I have repeatedly insisted on the fact that we are not to take mere reactions to sensory impressions as indications of true sensation. If they are to be so regarded, then we must clearly differentiate between sated. In the case of dogs, however, there is a very marked difference between lesions of the cortical motor centres and lesions of the corpus striatum. The affection of motility, from destruction of the cortical centres, is rather a paresis than a paralysis, and the affection is only of comparatively short duration. Carville and Duret have found that if the medullary fibres between the corpus striatum and the cortex are divided, the effect is just the same as if the cortical grey matter alone were destroyed, a result to be expected *à priori.* When, however, the section (see fig. 57, x) is carried through the corpus striatum, so as to destroy the fibres which descend from the convolutions, and also the connections proper of the ganglionic cells with the peduncular fibres (an operation which fulfils the conditions of real destruction of the corpus striatum, as I understand the term), complete hemiplegia is the result. The limbs are rendered entirely powerless, and lateral distortion of the body to the side of lesion, in the form of a curve, generally also occurs. The animal is unable to maintain its normal attitude, and falls helpless; or, if it attempts to move, it is impelled by the action of the unparalysed side to move round in a circle.

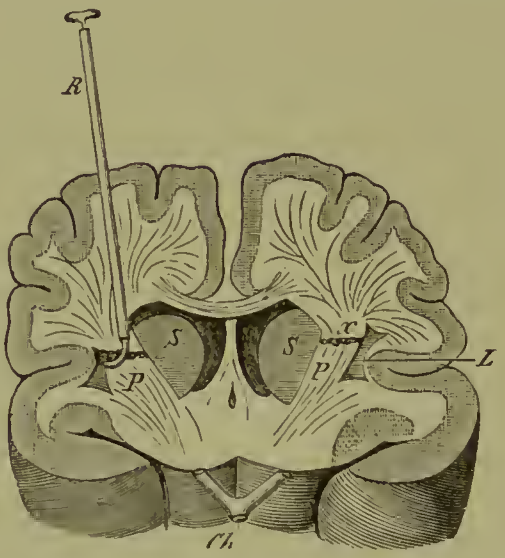


FIG. 57.—Vertical transverse section of the Brain of the Dog, five millimetres anterior to the Optic Commissure (Carville and Duret). S S. Nuclei caudati of the corpora striata. L. The lenticular nucleus. P P. The peduncular expansion. *Ch.* Optic chiasma. x. Section of the peduncular expansion causing *hemiplegia.* R. Veyssière's stylet for dividing the internal capsule.

The destruction of both corpora striata renders the animal utterly powerless and prostrate.

In rabbits, on the other hand, the destruction of the cortical motor centres produces less marked and more transient affection of motility than even in dogs. The destruction of the corpus striatum on one side, as Nothnagel's experiments and my own show, causes paresis of the opposite limbs and lateral distortion to the side of lesion, but the animal can still maintain its position on its feet and jump about, when stimulated, with comparative vigour and freedom of movement. When both corpora striata are destroyed the animal can still maintain its normal attitude, though the limbs, especially the anterior, tend to give way and sprawl.

The limbs may be placed in any position without the animal making any resistance or attempt to withdraw them, if this is done gently. But if the animal is pinched it springs away. An animal in which the corpora striata are both destroyed remains usually quite motionless unless it is disturbed, but I have seen one make spontaneous movements without any apparent source of external stimulation. And I have also observed evidence of the retention of appetite and desire to eat, by the irregular struggles and ineffectual attempts on the part of the animal to make the necessary movements to seize and masticate its food. A rabbit, therefore, in which the corpora striata alone are destroyed, differs essentially from one in which the cerebral hemispheres have been entirely removed, by the retention of spontaneity and internal springs of action (*vide* Chap. XI.)

§ 87. These relative differences in the effects of destruction of the cortical motor centres, and of the corpora striata in man, monkeys and rabbits, throw considerable light on the special functions of these ganglia.

In the rabbit the powers of co-ordinated locomotion are not abolished either by destruction of the corpora striata, or cortical centres, or both. In the dog the destruction of the corpora striata completely, for the time at least, paralyses all the powers of movement, which are only partially and transiently affected by removal of the cortical centres; while in the monkey and in man the destruction of the corpora striata adds but little to the completeness of the motor paralysis which results from extirpation of the cortical centres.

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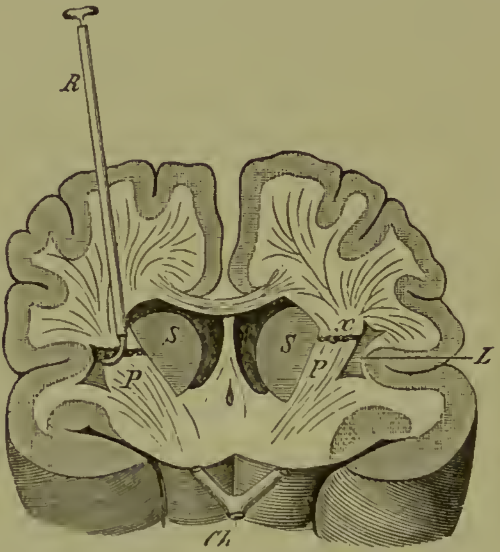

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These differences can only be satisfactorily accounted for on the principles already repeatedly enunciated—that animals differ greatly in respect to the degree in which the motor activities are independently organised in the mesencephalic and lower centres. This is much greater in the rabbit than in the dog, as is shown by the marked difference between the results of ablation of the cerebral hemispheres in these animals respectively. Movements at first requiring true volitional effort—by which is meant action conditioned by consciously discriminated impressions present or revived—tend to become automatic by repetition, and the less varied and complex the movements the more speedily does this automatic organisation become established.

It is evident from the facts of experiment on dogs that the corpora striata are the centres in which this organisation occurs. They form as it were the centres of automatic or sub-voluntary integration of the various voluntary-motor centres differentiated in the hemispheres.

The more complex and varied motor activities of man and the monkey are more dependent on truly conscious effort, and are longer in being acquired, and longer in being reduced to automaticity. Yet we know that by constant and habitual repetition, modes of action which were acquired by long and painful education and conscious effort, ultimately become so easy as to be performed without attention, if not absolutely without consciousness. We have reason, from the facts of comparative physiology, to regard the corpora striata as the centres in which these habitual or automatic movements become organised. The optic thalami play the same subordinate rôle to the sensory centres, which the corpora striata play to the motor centres of the hemispheres. That they are not the centres of true conscious activity is clearly proved by the facts already advanced, which show that the regions of true sensation are above these ganglia. But though the consciousness of sensory impressions must precede any truly volitional act in response thereto, we find that by education and frequent repetition, the action becomes so easy as to follow impression without conscious discrimination or attention, the nexus between impression and action becoming so organically welded in the sensory and motor centres as to assume the character of reflex reaction below the domain of consciousness. In this case we may suppose that impressions made on the organs of sense travel up to the optic thalami, and thence pass directly to the corpora striata, instead of taking the larger or conscious circle through the sensory and motor centres of the hemispheres. That this shorter or automatic circle is sufficient for purposes of locomotion in the dog, is shown by the fact that notwithstanding the interruption of the larger circle by excision of the cortical motor centres in this animal, movements in response to immediate impressions, or (when the sensory centres of the cortex remain) in response to ideal impressions, are still capable of being effected with tolerable precision and steadiness. The destruction of the corpora striata annihilates the centres of organisation of these motor activities, and the animal lies helpless and completely paralysed.

In man, however, the shorter circle through the optic thalami and corpora striata does not appear sufficient, for the interruption of the conscious circle through the hemispheres by lesion of the cortical motor centres produces paralysis of a very complete and enduring character.

This goes far to show that even the most habitual or most automatic actions of man require the co-operation of the centres of conscious activity, a view which is taken and strongly argued by Dr. Ireland. ('Can Unconscious Cerebration be Proved?' 'Journal of Mental Science,' October 1875.)

But though the basal ganglia may not of themselves suffice for the execution of the habitual movements in man, there is every reason for believing that they do so to a large extent, from the fact that the performance of habitual actions exercises but little interference with the conscious activity of the hemispheres in other directions.

We may express it thus, that in actions requiring conscious discrimination and voluntary effort, the larger circle of the hemispheres is involved, but that in the actions which have become habitual and automatic, the larger circle is greatly relieved by the organic nexus between impression and action, which has been established in the sensory and motor basal ganglia. The optic thalami and corpora striata form thus a *sensori-motor* mechanism, according to the views of Dr. Carpenter. I would use the term, however, only in the generic sense of *afferent-efferent*; it having been shown that sensation, or consciousness of impressions, is not a function of the optic thalami. Hence the reaction between the optic thalami and corpora striata being below the domain of consciousness, is outside the sphere of psychical activity properly so called.

CHAPTER XI.

THE HEMISPHERES CONSIDERED PSYCHOLOGICALLY.

§ 88. Hitherto we have considered the brain chiefly in its objective or physiological aspects, and the conclusion has been arrived at that the brain is a complex system of centres of motion and centres of sensation.

In their subjective aspect the functions of the brain are synonymous with mental operations, the consideration of which belongs to the science of psychology and the subjective method of investigation. No purely physiological investigation can explain the phenomena of consciousness. By throwing light, however, on the anatomical substrata of consciousness, physiological experiment may serve to elucidate some of the at present obscure relations between normal and abnormal conditions of the brain, and normal and abnormal psychical manifestations.

It is not the object of this work to attempt an analysis of mind or the laws of mental operations, but simply to discuss, in the light of the facts revealed by the experimental investigations recorded in the preceding chapters, some of those relations between the physiological and psychological functions of the brain which present themselves to the consideration of the physician and medical psychologist.

That the brain is the organ of the mind, and that mental operations are possible only in and through the brain, is now so thoroughly well established and recognised that we may without further question start from this as an ultimate fact.

But how it is that molecular changes in the brain cells coincide with modifications of consciousness; how, for instance, the vibrations of light falling on the retina excite the modification of consciousness termed a visual sensation, is a problem which cannot be solved. We may succeed in determining the exact nature of the molecular changes which occur in the brain cells when a sensation is experienced, but this will not bring us one whit nearer the explanation of the ultimate nature of that which constitutes the sensation. The one is objective and the other subjective, and neither can be expressed in terms of the other. We cannot say that they are identical, or even that the one passes into the other; but only, as Laycock expresses it, that the two are correlated, or, with Bain, that the physical changes and the psychical modifications are the objective and subjective sides of a 'double-faced unity.'

'We have every reason for believing that there is, in company with all our mental processes, *an unbroken material succession.* From the ingress of a sensation, to the outgoing responses in action, the mental succession is not for an instant dissevered from a physical succession. A new prospect bursts upon the view; there is a mental result of sensation, emotion, thought, terminating in outward displays of speech or gesture. Parallel to this mental series is the physical series of facts, the successive agitation of the physical organs. . . . While we go the round of the mental circle of sensation, emotion and thought, there is an unbroken physical circle of effects. It would be incompatible with everything we know of cerebral action, to suppose that the physical chain ends abruptly in a physical void, occupied by an immaterial substance; which immaterial substance, after working alone, imparts its results to the other edge of the physical break, and determines the active response—two shores of the material, with an intervening ocean of the immaterial. There is, in fact, no rupture of nervous continuity. The only tenable supposition is, that mental and physical proceed together, as undivided twins. When, therefore, we speak of a mental cause, a mental agency, we have always *a two-sided cause*; the effect produced is not the effect of mind alone, but of mind in company with body.' (Bain, 'Mind and Body,' 1873, p. 131.)

In accordance with this position it must follow from the experimental data that mental operations in the last analysis must be merely the subjective side of sensory and motor substrata. This view has been repeatedly and clearly enunciated by Hughlings-Jackson, with whose physiological and psychological deductions from clinical and pathological data I frequently find myself in complete accordance. ('Clinical and Physiological Researches on the Nervous System.' Reprints from 'Lancet,' 1873.)

§ 89. The physiological activity of the brain is not, however, altogether co-extensive with its psychological functions. The brain as an organ of motion and sensation, or presentative consciousness, is a single organ composed of two halves; the brain as an organ of ideation, or re-presentative consciousness, is a dual organ, each hemisphere complete in itself. When one hemisphere is removed or destroyed by disease, motion and sensation are abolished unilaterally, but mental operations are still capable of being carried on in their completeness through the agency of the one hemisphere. The individual who is paralysed as to sensation and motion by disease of the opposite side of the brain (say the right), is not paralysed mentally, for he can still feel and will and think, and intelligently comprehend with the one hemisphere. If these functions are not carried on with the same vigour as before, they at least do not appear to suffer in respect of completeness.

§ 90. In order that impressions made on the individual organs of sense shall excite the subjective modification called a sensation, it is necessary that they reach and induce certain molecular changes in the cells of their respective cortical centres.

If the angular gyrus (gyri) is destroyed or functionally inactive, impressions made on the retina and optical apparatus cause the same physical modifications as usual, but do not affect consciousness. The changes produced have no subjective side.

The optical apparatus without the angular gyrus may be compared to the camera without the sensitised plate. The rays of light are focussed as usual, but produce no chemical action, and leave no trace when the object is withdrawn, or the light from it shut off. The angular gyrus is like the sensitive plate. The cells undergo certain molecular modifications which coincide with certain subjective changes constituting the consciousness of the impression or special visual sensation. And as the sensitive plate records, in certain chemical decompositions, the form of the object presented to the camera, so the angular gyrus records in cell modifications the visual characters of the object looked at. We may push the analogy still further. Just as the chemical decomposition effected by the rays of light may be fixed and form a permanent image of the object capable of being looked at, so the cell modifications which coincided with the presentation of the object to the eye, remain permanently, constituting the organic memory of the object itself. When the same cell modifications are again excited, the object is re-presented or rises up in idea. It is not meant by this analogy that the objects are photographed in the angular gyrus, as objects are photographed on the plate, but merely that permanent cell modifications are induced, which are the physiological representatives of the optical characters of the object presented to the eye. The optical characters are purely light vibrations, and few objects are known by these alone. The object appeals to other senses, and perhaps to movements, and the idea of the object as a whole is the revival of the cell modifications in each of the centres concerned in the act of cognition. For what is true of the angular gyrus or sight centre is true, *mutatis mutandis*, of the other sensory centres. Each is the organic basis of consciousness of its own special sensory impressions, and each is the organic basis of the memory of such impressions in the form of certain cell modifications, the re-induction of which is the re-presentation or revival in idea of the individual sensory characters of the object. The organic cohesion of these elements by association renders it possible for the re-excitation of the one set of characters to recall the whole.

§ 91. The sensory centres, therefore, are to be regarded not merely as the organs of consciousness of immediate sensory impressions, but as the organic register of special sensory experiences. This organic memory is the physical basis of Retentiveness, and the property of re-excitability is the organic basis of Recollection and Ideation. We have thus a physiological foundation of the law arrived at on other grounds by Bain, *viz.* that 'the renewed feeling occupies the very same parts, and in the same manner as the original feeling.' According to Spencer, the renewal of the feeling is the *faint* revivification of the same processes which are *strongly* excited by presentation of the object. The molecular thrill, if we may so term it, of present sensation extending from the peripherical organ of sense, is in the ideal sensation revived, but, as a rule, not so powerfully as to extend to the periphery; though, in rare instances, the central revivification may be so intense as actually to re-induce the peripherical impression. This occurs in certain morbid states such as are described under the name of 'fixed ideas,' or in sensory hallucinations from diseased conditions of the brain, as in epilepsy and insanity.

The organic memory of sensory impressions is the fundamental basis of knowledge. If the sense impressions were evanescent, or endured only so long as the object was present, the range of conscious intelligent action would be limited to the present, and we should have no real knowledge. Knowledge implies the consciousness of agreement or difference. We can only be said to *know* when we recognise identity, or difference between past and present conscious modifications. We know that a certain colour is green by recognising a similarity or identity between the present and a certain past colour sensation, or a difference between this and some other colour in the spectrum. If we had no organic memory of the past capable of re-excitation to serve as the basis of comparison, we should be unable to recognise either agreement or difference. We might be conscious from moment to moment, but there would be no continuation in time, and knowledge would be impossible. The foundation of the consciousness of agreement is the re-excitation by the present of the same molecular processes which coincided with a past impression; and of difference, a transition from one physical modification to another. The sensory centres, therefore, besides being the organs of sensation or consciousness of immediate impressions, contain, in the persistence and revivability of the coincident physical modifications, the materials and possibilities of simple and complex cognitions, in so far as these are dependent on sensory experience alone.

The destruction of the sight centre, therefore, not only makes the individual blind presentatively, but blind re-presentatively or ideally, and all cognitions into which visual characters enter in part or whole become mangled and imperfect, or are utterly rooted out of consciousness. The destruction of the eye renders the individual blind only presentatively, but his visual memory and visual ideation remain unaffected. And it would be extremely interesting to ascertain whether, in an individual born blind, the sight centre (§ 65) presents any peculiarities either as regards the forms of the cells, or their processes or otherwise, differing from those of the normal brain. If such were detectable, we should come near arriving at the characters of the physical basis of an idea.

§ 92. Thus far with respect merely to the primordial elements of sensory ideation. It has been said by Aristotle, '*Nihil est in intellectu quod non prius fuerit in sensu*,' but this is true only in so far as man is regarded as a sentient and not an active organism. Man, however, is possessed both of passive, or sentient, and active, or motor, functions, and these latter have also their ideal side, and form an integral factor in the composition of mind..

If the dictum be read as implying that intellect begins with sensation, it may be accepted as true. The springs of conscious activity, or the incentives to volition, are present or ideally revived sensations and their accompaniments. Sensations are accompanied in consciousness by feelings which are divisible into two great classes, Pains and Pleasures. Just as sensations are the subjective side of certain physical modifications of the nerves and nerve centres, so pleasurable or painful sensations may be regarded as the subjective expression of physical harmony or disharmony between the organism and the influences acting on it. A painful sensation is a physiological discord incompatible with health or comfort; a pleasurable sensation is a physiological harmony promoting health and comfort. Bain expresses this fact as the law of self-conservation. 'States of Pleasure are connected with an increase, States of Pain with an abatement of some or all of the vital functions.'

As the revived or ideal sensation occupies the same parts as are concerned in the present sensation, so the revived feelings or emotions are localised in the same parts. The sensory, ideational and emotional centres are thus one and the same. The feelings accompanying the more intellectual senses, sight and hearing, are the primordial elements of the æsthetic emotions which are founded on harmonies of sight and sound.

§ 93. The senses differ greatly in respect to the relative preponderance of the intellectual, or discriminative, and emotional, or feeling, element in their composition, and in respect to their revivability as ideas or as feelings. In sight the emotional is subordinate to the intellectual, or may be almost entirely absent, and in the great majority requires cultivation; in the sensations of organic life the emotional is at its maximum, and the intellectual, or discriminative, at its minimum. Organic sensations generally, with one or two exceptions, unless rising to the pitch of painful intensity, are obscure and non-localisable, and the healthy or morbid physiological activity is expressed subjectively, as the vague and ill-defined feeling of well- or ill-being, '*euphoria*' or '*dysphoria*' (Laycock).

The organic sensations and their cerebral centres, probably the occipital lobes, would thus seem to be the foundation, or universal background, of the pleasurable or painful emotions in general. Morbid states of the viscera and of their cerebral centres are incompatible with pleasurable emotions of any kind. As healthy states of the viscera produce pleasurable feelings, and morbid states of the viscera produce painful or depressing feelings; so conversely, on the principle that the revived feeling occupies the same parts as the original, pleasurable emotions exalt the vital functions, and painful emotions depress the vital functions and produce organic visceral derangements. Whether the various viscera are represented individually in the cerebral hemispheres has not been experimentally ascertained. It is, however, not improbable; and the ancient localisation of certain emotions in certain viscera, though crude, is not without some foundation in positive physio-psychological fact. Morbid states of the viscera, or of the centres of organic sensations in reciprocal action and reaction, may give rise to hypochondriasis or melancholia; and just as visceral derangements frequently express themselves in localisable sympathetic neuroses, so the melancholic individual projects the obscure feelings in some definite objective form as the cause of his sufferings. He imagines that his vitals are being gnawed at by some hideous animal, or that his body is the scene of demoniacal revels. The special form of the hallucination will vary with the individual and his education, but it always takes some dread or malignant shape.

§ 94. The physiological needs of the organism, in so far as they induce locally discriminable sensations, express themselves subjectively as definite appetites or desires, which are the conscious correlations of physiological wants. The appetite of hunger is the desire to satisfy a local sensation, referable to the stomach, in which the physiological needs of the organism centre themselves. The basis of the feeling of hunger and the appetite for food is the stomachic branches of the vagus, and the cerebral centres of the same. And as local conditions of the stomach may destroy or increase the feeling of hunger, so central disease may give rise to ravenous appetite, or sitophobia, conditions exemplified in insanity.

The bodily need of water expresses itself locally in a dry condition of the fauces, which is the basis of the feeling of thirst and the appetite for drink. The sensations in this case, however, are more tactile than purely organic, and this may account for the fact that lesions, which cause abolition of the appetite for food, such as we have seen to result from extensive destruction of the occipital lobes, do not abolish the appetite of thirst.

The sexual appetite, though springing from the organic wants of certain glandular structures, centres itself round a certain tactile sensation, which is the reflex key to the gratification of the physiological demand for functional exercise on the part of these organs. The sexual appetite appears only with the development of the generative glands. Its appearance induces considerable perturbation of the other organic functions, and expresses itself subjectively at first chiefly in the form of emotional excitability, or in obscure longings, morbid desires, or hysterical outbursts. Long before the link between a definite sensation and a definite action for its realisation has been established in consciousness, the generative glands may gratify themselves reflexly during sleep, the period, *par excellence*, of reflex excitability.

As morbid irritation of the generative organs may excite a morbid sexual appetite, so conversely, the sexual appetite may be morbidly excited by pathological irritation of the cerebral paths and cerebral centres of the sensations connected with the exercise of the generative functions. To the former belong the satyriasis or nymphomania occasionally observed in connection with disease of the middle lobe of the cerebellum; to the latter the various morbid exhibitions of the sexual appetite in insanity, where the centres are functionally or organically diseased. From certain facts of experiment, we have seen reason to conclude that the centres of sexual feeling are probably localisable in the regions connecting the occipital lobes with the lower and inner part of the temporo-sphenoidal lobe.

As the reproductive organs in women form such a preponderant element in their bodily constitution, they must correspondingly be more largely represented in the cerebral hemispheres, a fact which is in accordance with the greater emotional excitability of women, and the relatively larger development of the posterior lobes of the brain.

§ 95. The various sensations, feelings and desires present or revived in idea, singly or in associated combinations, form the incentives to action, the motives to volition.

The outward expression of certain physiologically painful or pleasurable sensory impressions, takes place instinctively or independently of individual education, their realisation in consciousness, as pleasurable or painful sensations, merely coinciding with, or in strict accuracy following, their manifestation in action. Such are the reflex spinal actions, and the reflex expressions of emotion, which, as we have seen, are capable of being manifested through the optic lobes and mesencephalic centres, independently of the hemispheres.

All truly voluntary action, on the other hand, is the result of education, the duration of which varies within extremely wide limits in different classes of animals, and in respect to individual acts of volition in the same animal.

At birth the human and the monkey infant have no volition; they have only the elements of its composition.

The actions of the infant are at first limited to definite reflex response to definite external or internal stimuli, and to indefinite or general motor activity, conditioned not so much by any definite stimulus as by a natural tendency of the nerve centres to expend their surplus energy in action. To this latter tendency Bain gives the name 'spontaneity.' Though it is impossible to say how far this expenditure of energy is dependent on central impulse alone, and how far on external and internal sensory impressions in general acting on the nerve centres, the term spontaneity sufficiently well expresses a definite physiological fact of the constitution.

Actions determined reflexly, or originating spontaneously, according as they prove physiologically beneficial and subjectively pleasurable, tend to continuance and repetition; while actions physiologically hurtful and subjectively painful, are checked or avoided.

The conscious discrimination of a sensation as pleasurable, and its ideal persistence as desire, and its association with things seen, smelt or tasted, are effected long before the sensation, present or revived, is associated with any differentiated motor act for its accomplishment or realisation. This latter is the result of happy accident, or of repeated trials and error. Though the child possesses in the motor centres of its cerebral hemispheres the potentiality of differentiated motor acts, the individual selection, or excitation, of any one of these, in response to a present or revived sensation, requires the establishment, by education and repetition, of an organic nexus between the special sensory centre or centres, and the special motor centre. Some particular object held before a child recalls by sight a pleasurable sensation, and excites desire ; but, instead of inducing, as yet, a definite action for its gratification, excites only vague and undefined movements of arms, legs and facial muscles, the expression of general excitation of the motor centres. In process of time the centre of the special differentiated movement necessary to the gratification of the desire can be thrown individually into action, and thus a definite act of volition is, for the first time, fairly accomplished. Voluntary control is first established over those movements, which are also most easily called into play by reflex stimulation.

A child can voluntarily grasp with its fist long before it can raise its hand to its mouth, or put out its hand to lay hold of anything. This is parallel with the fact that the hand can be made to close reflexly over any object placed in the palm, long before the same action can be performed voluntarily. And it is curious and interesting to observe in a child, how, in the growth of volition, the first action fairly differentiated in response to any particular sensation or desire, is repeated in response to desire in general, however ludicrously insufficient to accomplish the desired end. The individual activity of the various specially differentiated motor centres having once been fairly established at first in response to particular sensations and desires, voluntary acquisition proceeds apace, the centres being free to form new associations and become the means of realisation in action of all the varied simple and complex impulses of the sensory centres. The associating fibres between the one motor centre and the various sensory centres may thus become innumerable.

The rate at which the organic nexuses are established between the sensory and motor centres varies according to the degree of complexity and intricacy of the movements. Complex and intricate movements are longer in being acquired than those which are simple, and also reflex or already hereditarily organised. Hence the movements of articulation in combination with those of vocalisation are longer in being acquired than those of the arms or legs. In the lower animals the control and co-ordination of movements are almost complete at birth, or require little education as compared with the prolonged helplessness of the human infant.

Some birds start from the egg already fully equipped, like Athene from the head of Zeus.

They are in great measure mere 'conscious automata.' They are capable of acquiring sensory experience and association of ideas, but of little further motor acquisition beyond that with which they start in life. Their cortical motor centres count for little, and may be removed without causing much disturbance of their ordinary modes of activity. Rabbits require but comparatively short education to perfect their powers; cats and dogs longer; but cats and dogs are already advanced in life, and have assumed the cares of paternity, or rather maternity, when the human infant can scarcely lift a finger in its own behalf.

In proportion as volition predominates over conscious automatism, is education necessary to perfect the powers of movement; in the same proportion are the cortical motor centres developed; and in that proportion are the powers of movement paralysed by destruction of the motor centres of the hemispheres.

In the rabbit conscious-automatism is more marked than in the dog; the period of education is shorter; the faculty of further special motor acquisition is small; the cortical centres are but lowly developed; and their removal exercises but slight and transient disturbance of their ordinary modes of action. In the dog volition enters more largely into the motor activities; the period of education is longer; the faculty of special motor acquisition beyond the mere power of locomotion is greater; the cortical motor centres are more highly developed, and their removal causes greater disturbance of their motor powers, not however permanently paralysing their conscious-automaticity, but abolishing their special voluntary motor acquisitions. In man volition is predominant; education is long and laborious; the faculty of special motor acquisition is unlimited; the cortical motor centres reach their highest development; and their removal causes such complete and enduring motor paralysis as to indicate that automatism in and by itself is scarcely detachable from the centres of consciousness and volition.

§ 96. In the same manner as the sensory centres form the organic basis of the memory of sensory impressions, and the seat of their re-presentation or revival in idea, so the motor centres of the hemispheres, besides being the centres of differentiated movements, are also the organic basis of the memory of the corresponding movements, and the seat of their re-execution or ideal reproduction. We have thus a sensory memory, and a motor memory, sensory ideas and motor ideas; sensory ideas being revived sensations, motor ideas being revived or ideal movements. Ideal movements form no less an important element in our mental processes than ideally revived sensations.

Man is not merely a passive or receptive organism capable of registering impressions on his organs of sense in the form of sensory ideas or feelings, but also an active or executive organism, possessing the power of varied and complex forms of motor activity. These motor activities, called into play by definite feelings or sensations, actual or revived, constitute volitional movements, and the organic cohesion formed between the sensory and motor centres persistently enduring in these centres, is the physical basis of our volitional acquisitions in all their manifold range and complexity. The motor centres and motor facultics, besides furnishing the conditions and possibilities of multiple and varied voluntary movements, and the organic registration of these as motor or mechanical acquisitions, enormously widen the field of sensory experience and complicate its results. By the movements of the head and eyes we greatly extend the scope and complicate the facts of visual sensation, and by the movements of the limbs the range of tactile experience is increased a thousandfold.

There are few objects of cognition known to us only by sensory characters or impressions. The vast majority involve the activity both of our sensory and motor faculties, and our ideas are a mixed revival both of ideal movements and ideal sensations in their respective coherent associations. This is exemplified in the acquisition and constitution of ideas of form, shape, weight, resistance, and the like.

Our ideas of form are not mere revived optical impressions, which are properly limited to colour (except perhaps in so far as the object viewed does not subtend a visual angle larger than can be included easily within the punctum centrale retinæ), but optical impressions, combined with ideal ocular movements. Our idea of a circle is a combination of an ideal coloured outline with an ideal circular sweep of the eyeballs, or it may be, of the tactile impressions coinciding with an ideal circumduction of the arm or hand, or perhaps both these factors combined. The same elements enter into all varieties of form or shape of which we are capable of forming an idea. Our ideas of distance, weight, resistance, all involve not merely sensory factors, but these combined with muscular movements. To revive any of these ideas, is to revive both the sensory and motor elements of their composition, and we tend in ideation to repeat the actual movements which were concerned in the primary act of cognition. Ideas, therefore, except in so far as they are simple revivals of definite and uncomplicated sensory impressions or motor acts, have no circumscribed habitation in the brain, but are the re-excitation of each and every one of the sensory and motor centres which are specially concerned in their acquisition. We know an orange by certain discriminated impressions made on the organs of sight, smell, taste, touch, and by certain muscular movements and sensations which give the form; and the re-presentation or idea of an orange is the associated re-excitation of the permanent cell-modifications, in each of the special sensory and motor centres primarily engaged in the act of cognition.

There is practically no limit to the number of associated combinations of sensory and motor elements. Sensory centres form organic associations with other sensory centres; motor centres with motor centres; sensory centres, simple and in complex association, with simple or complex associations of motor centres. In this variety and complexity of permanent modifications, and organic cohesions between the sensory and motor centres of the hemispheres, we have the basis of all intellectual and volitional acquisitions. Each motor centre may enter into organic association with each and every sensory centre, each definite association being the representative of some consciously discriminated act. In the variety of associations between movements and sensations, some are loosely, some more firmly coherent; while one sensori-motor association is so constant as to give rise to the notion that the connection is indissoluble. This is the association between muscular movement and muscular sense, one in normal conditions so constant as to lead Bain to suppose that the latter is the inseparable concomitant of the motor impulse. I have endeavoured to show that the connection, though constant, is not inseparable, a distinction by no means a matter of hypercritical refinement, but a fundamental one, and one carrying with it the most important physiological, as well as psychological issues.

The sensations accompanying muscular action being repeated as often as the muscular action itself, the organic nexus between the motor and tactile centres becomes so welded that this sensori-motor cohesion enters, like a compound chemical radical, as a simple factor, into every association which motor centres can form with other motor centres, and with sensory centres in general. Hence, in all volitional movements, the tactile sensory centres invariably functionate along with the motor centres, and give the extent and degree of the movement actually, or ideally carried out. Bain would make the sensory a *proprium* of the motor, whereas it is only a contingent: in normal or physiological conditions an inseparable accident; but separable anatomically and pathologically.

In the process of volitional acquisition the cohesions are chiefly formed between sensations and right-sided movements, so that the organic nexuses are established principally between the sensory centres and the motor centres of the left hemisphere, by which the movements of the right side are effected and governed.

§ 97. The growth of volition, the formation of permanent motor acquisitions, and the establishment of organic cohesions between the sensory and motor centres of the cerebral hemispheres are well illustrated in the acquisition of articulate speech. Commencing with spontaneous vocalisation and spontaneous movements of the articulatory apparatus, and encouraged and aided by imitative repetitions on the part of its teacher, the infant gradually acquires the power of associating a certain sound with a certain articulation, so that on the given sound the appropriate movements of the articulating and vocalising apparatus are called into play to reproduce it. An organic nexus becomes firmly established between the auditory and the articulating centres, and such nexuses become multiplied indefinitely, each articulate sound being represented by a definite sensori-motor cohesion—sound-articulation.

A further development of sensori-motor acquisition is the gradual establishment of links of association between certain visible characters and certain articulations, and this in such a manner that a certain visible symbol is recognised as the equivalent of a certain auditory impression, so that either can call up the proper articulation with definiteness and precision.

Here the rticulatory or motor element is the central point of two sensory cohesions, the one auditory, the other visual, which two are regarded as equivalent.

In the case of the blind a similar cohesion may be formed between certain tactile impressions, and the centres of articulation, so that at a definite tactual impression, as well as at a definite auditory impression, a definite articulate combination is called forth.

A still farther stride in complexity is the acquisition of the power to represent by movements of the fingers, symbols which, when seen, call up by association certain sounds and articulations.

Organic nexuses thus become established between the centres of hearing and articulation, between those of sight and articulation, or between those of touch and articulation; and complex nexuses between the centres of sight and sound, and the motor centres of articulation and manual movements.

These organic nexuses correspond to the acquisitions of spoken and written language, and the art of writing.

It is conceivable that all these simple and complex acquisitions and cohesions might be formed without any association having been established between certain articulate sounds or written symbols, and certain objects or ideas; or, in other words, both spoken and written language might be acquired altogether apart from things signified. For the connection between words and things signified is nothing more than an association; words in themselves being only symbols. The association of articulate sounds with things signified is, however, generally preceded by, and proceeds *pari passu* with the growth of the faculty of speech, so that the cohesion between the centres of hearing and articulation is rendered complex by the association of definite articulate sounds with certain objects seen, heard, touched, smelt or tasted, or with objects of cognition in general.

Hence the articulation may be called into play not merely by a certain sound, but by the actual presentation or representation of the object signified. The centres of articulation become, therefore, the central motor point of an immense number of sensory cohesions, all of which tend to evoke the articulation, and which, in turn, tend to be revived in idea by the actual or ideal articulation itself. The articulation is the essential fact, vocalisation being subordinate, and capable of being dispensed with altogether, as in whisper speech.

The primary associations in the acquisition of articulate speech being between sounds and articulations, as in spoken language, or between visible signs and articulations, as in written language, and between both these and things signified—directly in the former, and indirectly in the latter—secondary associations may be formed between visible signs and things signified, the link through articulation becoming subordinate, if not entirely dispensed with. A sound readily calls up the thing signified, without the intervention of an articulation. It is, however, less common for a visible symbol to call up the thing signified without the intervention of an articulation, more or less suppressed. In the great majority of people there is observable a tendency, during reading, to translate the written symbols into their equivalent articulations. The less educated the person, and the less accustomed to reading, the greater is this tendency exhibited; and some persons cannot read intelligently without actually going through all the processes of articulation represented by the written characters.

§ 98. If the motor centres of the cerebral hemispheres are not merely the centres of impulse of volitional movements, but also the centres of registration and revivability of the same, it must follow that destruction of the cortical motor centres will cause not only objective motor paralysis, but subjective motor paralysis, or in other words, paralysis of motor ideation.

If an individual should by education acquire the faculty of expressing his thoughts by symbolic dextral movements, the destruction of the manual motor centres of the left hemisphere will not only cause paralysis of the right hand, but also annihilate in ideation the association between thoughts and dextral movements. If a blind deaf-mute like Laura Bridgman were to associate thoughts and ideas with symbolic movements of the right hand in particular, such a person would be rendered not merely hemiplegic, but aphasic, by reason of destruction of the manual motor centres in the left hemisphere.

For the registration and ideal revival of volitional movements must take place in the same centres as are primarily and specially engaged and educated.

Hence the memory and revivability in idea of volitional movements must, as far as relates to the hand and arm, be principally in the left hemisphere, seeing that volitional education and motor acquisitions are in the great majority of people a matter of right-sided development.

The motor centres of articulation present certain peculiarities, both in their physiological and psychological aspects.

Physiologically, the centres of articulation have a bilateral action, as I have experimentally demonstrated; the centre in one hemisphere being sufficient to innervate the muscles of articulation on both sides. Hence, destruction of the centre of articulation in one hemisphere does not cause paralysis of articulation, but only, if anything, a paresis of action on the opposite side.

But while as regards the mere physiological excitation of the muscles of articulation, there seems to be little or no difference between the centres of articulation in the right and left hemisphere, there is a marked difference between the two as regards the registration and ideal reproduction of articulatory movements.

§ 99. In the remarkable and, in a physio-psychological sense, highly instructive condition termed aphasia, many of the principles above laid down are strikingly exemplified.

The subject of aphasia is deprived of the faculty of articulate speech, and also very generally of the faculty of expressing his thoughts in writing, while he continues intelligently to comprehend the meaning of words spoken to him, or, it may be, to appreciate the meaning of written language. An aphasic individual knows perfectly well, as exhibited by his gestures, if a thing is called by its right name or not, but he cannot utter the word himself, or write it when it is suggested to him. In his attempts, only an automatic or interjectional expression or some unintelligible jargon escapes his lips, or unmeaning scrawls are set down on paper as writing.

This affection is usually, at first at least, associated with a greater or less degree of right hemiplegia, but the motor affection of the right side, chiefly of the right arm, is often slight and transient, or may be wanting from the first, the only indication of motor paralysis being a paretic or weak condition of the oral muscles of the right side.

The inability to speak is not due to paralysis of the muscles of articulation, for these are set in action and employed for purposes of mastication and deglutition by the aphasic individual.

The cause of this affection was shown by Broca—and his observations have been confirmed by thousands of other cases—to be associated with disease in the region of the posterior extremity of the third left frontal convolution, where it abuts on the fissure of Sylvius, and overlaps the island of Reil, a region which I have shown corresponds with the situation of the motor centres of articulation in the monkey (see fig. 63, 9 and 10).[1]

One of the most common causes of the affection is softening of this region, consequent on sudden stoppage of the circulation by embolic plugging of the arterial channels which convey its blood supply, by which the functional activity of the part is temporarily or permanently suspended.

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[1] I do not consider it necessary, in the present state of clinical medicine and pathology, to enter at length into cases and arguments in favour of the definite localisation of the lesion causing aphasia. I take it as established beyond all possibility of doubt, that lesions in the region indicated above do in the overwhelming majority of instances cause aphasia, and the problem before us is to explain why such lesions should cause aphasia and leave other faculties intact. It is utterly beside the point to argue that loss of speech is not in all cases due to localised disease of this nature, for naturally, whatever causes paralysis of the muscles of articulation will cause inability to speak; and whatever interrupts the processes of ideation and thought, such as sudden shocks of emotion or the like, will also cause inability to speak. Such states cannot properly be classed under the head of aphasia, where we have a definite condition of loss of speech, while all other faculties, sensation, emotion, thought and volition remain practically unimpaired.

In reference to the arguments of the opponents of localisation, if such still exist, I would quote with the fullest concurrence the following passage from Dr. Broadbent, written in 1872, which the observations of the intervening years only serve to corroborate and confirm. 'The question being one of primary interest in cerebral physiology, I have examined all the apparently exceptional cases of which I have been able to find the published record; and it is remarkable how large a proportion of them break down under careful scrutiny. Setting aside the distinction between the conditions to which the terms amnesia and aphasia have been applied, I have found, described under the head of aphasia, cases of labio-glosso-pharyngeal paralysis on the one hand, and of dementia on the other, and again, the speechlessness or indistinct articulation of patients who have never fully recovered from the shock of an apoplectic or convulsive attack, or of embolism of a large cerebral artery. Cases are quoted as examples of aphasia without disease of the left third frontal convolution, in which the left middle cerebral artery, the nutrient vessel of the part, was blocked up; in which, therefore, the persistence of speech would have constituted a graver objection to the views in question, than its loss; or in which, without apparent disease of the surface grey matter, the convolution was cut off from the central ganglia and the rest of the cerebrum by lesion of its white fibres; in some instances again, aphasia has been fugitive, and therefore dependent on some temporary condition; and yet the cases have been considered exceptional because no permanent lesion has been found after death. On the other hand, cases have been described as examples of disease of the left third frontal gyrus without affection of speech, in which the description of the lesion clearly shows that the observer has taken some other convolution for the one named.' ('Mechanism of Thought and Speech,' *Medico-Chirurgical Transactions*, vol. lv. 1872.)

Owing to the proximity (*vide* fig. 63) and common vascular supply of the motor centres of the hand and facial muscles, it is easy to see how they also become implicated in the lesion of the centres of articulation, and why, therefore, dextral and facial motor paralysis should so commonly occur along with aphasia. This may be taken as further evidence in proof of the fact that lesions of the cortical motor centres cause motor paralysis on the opposite side.

The escape of the articulatory muscles from paralysis in unilateral lesion of the centres of articulation is accounted for by the bilateral influence of each centre which has been experimentally demonstrated.

The loss of speech actually or in idea from destruction of the centres of articulation is not more difficult of explanation on the principles laid down in this chapter, than the loss of sight presentatively or re-presentatively from destruction of the angular gyri. That which constitutes the apparent difficulty is the explanation of speechlessness without motor paralysis from unilateral lesion of the centres of articulation in the left hemisphere.

This difficulty is explicable on the principles laid down in reference to motor acquisitions in general. As the right side of the body is more especially concerned in volitional motor acts, so the education is principally in the motor centres of the left hemisphere, and these centres are more especially the organic basis of motor acquisitions. The left articulatory centres, as has been argued by more than one observer, preponderate over the right in the initiation of motor acts of articulation. They are, therefore, more especially the organic basis of the memory of articulations and of their revival in idea. The destruction of the left articulatory centres removes the motor limb of the cohesions which have been formed by long education between the centres of hearing and sight, and between the centres of ideation in general.

Sounds actual or revived fail to excite corresponding articulations actually or in idea. The individual is speechless, the motor part of the sensori-motor cohesion, sound-articulation, being broken. The sight of written symbols also fails to reproduce the equivalent articulatory action, actually or in idea. The individual is speechless, because the motor element of the sensori-motor cohesion sight-articulation is broken.

Ideally revived sights, sounds, touches, tastes, smells fail to call up the symbolic articulations, hence the individual cannot express his ideas in language, and in so far as language or internal speech is necessary to complex trains of thought, in that proportion is thought impaired. Thought, however, may be carried on without language, but it is thought in particulars, and is as cumbrous and limited as mathematical calculations without algebraical symbols. Thought, as has been observed by Bain, is in a great measure carried on by internal speech, *i.e.*, through the ideal or faint re-excitation of the articulatory processes which are symbolic of ideas. This is shown by the unconsciously executed movements of the lips and tongue which all persons exhibit more or less, and some so obviously that the unconscious processes rise almost to the point of whispering. So also the blind deaf-mute Laura Bridgman, whose language was symbolic movements of the fingers, during thought or when dreaming, unconsciously executed the same movements as she was accustomed to make in the actual exercise of her manual speech.

And just as ideas tend to excite their symbolic representations in articulation or in manual movements, so does the actual or ideal revival of the articulatory or manual movements tend by association to call up the other limbs of the cohesions, whether simple sights, sounds, tastes, smells, or their combinations. The importance of this connection between the articulating centres and the centres of ideation in general, will be shown more fully in reference to the voluntary revival of ideas and control of ideation (p. 285).

§ 100. We have seen that a person aphasic from destruction of his speech centre (as we may for shortness call the articulatory motor centres of the left hemisphere) still remains capable of appreciating the meaning of words uttered in his hearing. In this respect he does not (and there is no reason why he should) differ from a normal individual. His centres of sight, hearing, etc., being unimpaired, he is as capable as before of sight, auditory, tactile, gustatory and olfactory ideation. The difference consists in the fact that in the aphasic individual the word spoken, though it calls up the idea or meaning, cannot call up the word itself actually or in idea, owing to the centres of word execution and word ideation being destroyed. The appreciation of the meaning of spoken words is readily accounted for by the fact that in the process of education an association is formed directly between certain sounds and certain objects of sense, simultaneously with, if not antecedent to, the formation of the cohesive association between these sounds and certain acts of articulation. The cohesion or association between sound and meaning remains unimpaired in aphasia; it is the cohesion between sound and articulation which is broken, by removal of the motor factor of the organic nexus.

The association between visible symbols and things signified is, however, secondary to the associations formed between sounds and things signified, and between sounds and articulations, for speech precedes the art of writing. In the first instance, when an individual is learning to read, visible symbols are translated into articulations and revived sounds before they call up the things signified. This translation occurs in all at first, and continues apparent in those persons not much accustomed to reading, for they only understand by articulating in a more or less suppressed manner all the while. Just as an individual in learning a foreign language is at first obliged to translate the words into his vernacular before he reaches the meaning, but comes by familiarity and practice to associate the new words with their meaning directly without the aid of the vernacular, and even to think in the new language, so it is possible that by long experience in reading, a direct association may be established between visible symbols and things signified, without the mediation of articulation. In such a case a person who has his speech centre disorganised will still be able to comprehend the meaning of written language. A person, on the other hand, who has not established the direct association between visible symbols and things signified, and is still obliged to translate through articulation, will, by destruction of his speech centre, fail to comprehend written language, though he may still understand spoken language.

In learning to write a new association has to be grafted on to the association already formed between sounds and articulations. The new cohesion is between sounds and certain symbolic manual movements guided by sight, which symbolic tracings are the equivalents of certain acts of articulation. In the first instance this association between sounds, or sounds and things signified, and manual movements, takes place through the mediation of the centres of articulation, for the sounds or ideas are first reproduced actually or internally by articulations before their equivalence in written symbols is established and recognised.

By education, and by the familiarity engendered of long practice in expressing ideas by written symbols, a direct association becomes established between sounds and ideas, and symbolic manual movements, without the intermediation of articulation; and in proportion as the translation through articulation is dispensed with, in that proportion will an individual continue able to write who is aphasic from disease of his speech centre.

In the great majority of cases of aphasia, met with in hospitals, the direct association between sounds and ideas and manual equivalents of articulations has not been established, except for very simple and constantly repeated acts of writing such as signing one's name; and hence, as the intervention of articulation is still necessary before ideas can be expressed in writing, destruction of the speech centre causes not merely aphasia, but also *agraphia.*

Examples of all these different conditions are to be met with in aphasia. Some can neither speak nor write; some can write but cannot speak; some can write their names but cannot write anything else; all can comprehend spoken language; many can comprehend written language; others not at all, or very imperfectly. Between the normal condition of the speech centre and its total destruction, many intermediate abnormal conditions occur, which exemplify themselves as partial aphasia, and partial disorders of speech. In some cases there seems to be such a perturbation of the centres, that though the individual is not aphasic in the sense of being speechless, yet the associations between certain articulations and certain ideas are so disturbed that in attempts to speak only an incoherent jumble of words comes forth. This is a condition of ataxia rather than aphasia in the proper sense of the term.

The speech centre is, as has been stated, in the great majority of instances situated in the left hemisphere. But there is no reason, beyond education and heredity, why this should necessarily be so. It is quite conceivable that the articulating centres of the right hemisphere should be educated in a similar manner. A person who has lost the use of his right hand may by education and practice acquire with his left all the cunning of his right. In such a case the manual motor centres of the right hemisphere become the centres of motor acquisitions similar to those of the left. As regards the articulating centres, the rule seems to be that they are educated, and become the organic seat of volitional acquisitions on the same side as the manual centres. Hence, as most people are right-handed, the education of the centres of volitional movements takes place in the left hemisphere. This is borne out in a striking manner by the occurrence of cases of aphasia with left hemiplegia in left-handed people. Several cases of this kind have now been put on record. (*Vide* Thèse Mongié, Paris, 1866; quoted by Lépine, 'La Localisation dans les Maladies Cérébrales,' Paris, 1875. Russell, 'Med. Times and Gazette,' July 11, Oct. 24, 1874. Case (unpublished) communicated to me by my friend Dr. Lauder Brunton, of St. Bartholomew's Hospital.)

These cases more than counterbalance any exception to the rule that the articulating centres are educated volitionally on the same side as the manual motor centres. The rule need not be regarded as absolute, and we may admit exceptions without invalidating a single conclusion respecting the pathology of aphasia as above laid down.

Though the left articulatory centre is the one commonly and specially educated in speech, it is quite conceivable that a person who has become aphasic by reason of total and permanent destruction of the left speech centre, may reacquire the faculty of speech by education of the right articulatory centres. To a certain extent they have undergone education along with those of the left through associated action, registering automatically, as Hughlings-Jackson puts it, the volitional acts of the left. This automatic may be educated into volitional power, though at the age at which aphasia usually occurs, there is less capacity and plasticity in the nerve centres for forming new cohesions and associations. The rapid recovery which so frequently occurs in cases of aphasia, especially of the kind due to embolic plugging of the nutrient arteries of the left centres, is not so much to be regarded as an indication of the education of the right centres, but rather of the re-establishment of the circulation and nutrition in parts only temporarily rendered functionless.

But there are other cases which would seem to show that recovery of speech may take place after a lesion which has caused complete and permanent destruction of the left speech centre. A case which seems to me to be of this nature has been reported by Drs. Batty Tuke and Fraser ('Journal of Mental Science,' April, 1872), who, however, have adduced it as an instance opposed to the localisation of a speech centre, which in one sense, *i.e.*, as against absolute unilateral localisation, it certainly is. The case in essentials is that of a female patient who was rendered unconscious by the occurrence of cerebral hæmorrhage. On her recovery she was found totally speechless, and she remained so for an indefinite period. In process of time, however, the faculty of speech was restored in great measure, though never quite perfectly. 'During the whole period of her residence two peculiarities in her speech were observed—a thickness of articulation resembling that of general paralysis, and a hesitancy when about to name anything, the latter increasing very much some months previous to her death.

'The thickness seemed apparently due to slight immobility of the upper lip when speaking, but there was no paralysis when the lip was voluntarily compressed against its fellow. The inaction of the upper lip was observed by all.

'The hesitancy was most marked when she came to a noun, the hiatus varying in duration according to the uncommonness of the word. Latterly, she could not recall even the commonest terms, and periphrases or gestures were used to indicate her meaning. She was always relieved and pleased if the words were given her, when she invariably repeated them. For example, she would say, "Give me a glass of——" If asked if it was "water?" she said, "No." "Wine?" "No." "Whisky?" "Yes, whisky." *Never did she hesitate to articulate the word when she heard it.*'

Death occurred fifteen years after the seizure, and it was found *post mortem* that there was total destruction and loss of substance in the cortical region in the left hemisphere corresponding with the position of the centres of articulation (fig. 63, 9, 10). This seems to me one of the clearest cases of re-acquisition of the faculty of speech by education of the articulating centres of the right side. That speech was lost in the first instance is in harmony with the usual effect of lesion of the left speech centre. Education of the right side had not become quite perfect even after fifteen years, and that peculiar hesitancy, and the fact, which the authors themselves have specially noted in italics, that speech often required the aid of suggestion, is in accordance with the less volitional and greater automatic power of the right hemisphere. Aphasia being essentially due to the destruction, temporary or permanent, of the centres of excitation and organic registration of acts of articulation, is a significant proof of the fact that there is no break between the physiological and psychological functions of the brain, and that the objective and subjective are not separated from each other by an unbridgeable gulf.

§ 101. We have now traced the development of the volitional control of the movements, and the mode in which the memory of volitional acts becomes organised in the motor centres. The conclusion reached is that the volitional control of the movements becomes established when an organic cohesion is welded between a consciously discriminated feeling and a definite and differentiated motor act. The volitional control of the individual movements having once been established the work of education advances, and the conditions of volition become more and more complex. The volition of the untutored and inexperienced infant is of a more or less impulsive character, its action being conditioned mainly by impressions or ideas of the moment. Associations have not yet been formed between the pleasurable and painful remote consequences of actions. *Experientia docet.* A child which has acquired the differentiated control of its hands is impelled to touch and handle whatever strongly attracts its sight. The sight of a bright flame stimulates a desire to handle it. This is followed by severe bodily pain, and an association is formed between touching a certain brilliant object and severe suffering. The vivid memory of pain experienced on a former occasion, is sufficient to counteract the impulse to touch when the child is again placed in similar circumstances. Here we have a simple case of the conflict of motives, and the inhibition or neutralisation of one motive by another and stronger. Action, if it results at all, is conditioned by the stronger. Similarly, a hungry dog is impelled by the sight of food to seize and eat. Should the present gratification bring with it as a consequence the severe pain of a whipping, when certain articles of food have been seized, an association is formed between eating certain food and severe bodily pain; so that on a future occasion the memory of pain arises simultaneously with the desire to gratify hunger, and, in proportion to the vividness of the memory of pain, the impulse of appetite is neutralised and counteracted. The dog is said to have learnt to curb its appetite.

As experience increases, the associations between acts and consequences increase in complexity. Both by personal experience, as well as by the observed experience and testimony of others, associations are established between actions and their remote consequences as pleasures or pains, and it is found that present gratification may bring a greater and future pain, and actions causing present pain may bring a greater pleasure. As the great law of life is *vivere convenienter naturæ*—to secure pleasure and avoid pain in the highest and most general sense, and not for the moment only (a law which cannot be transgressed with impunity)—actions are conditioned no longer, as in the infant or untutored animal, by present desires or feelings alone, but by present desires modified by the ideally revived feelings of pleasure or pain near and remote, which experience has associated with definite actions. The motive to action is thus the resultant of a complex system of forces; the more complex, the wider the experience, and the more numerous the associations formed between actions and their consequences, near and remote. Actions so conditioned are regarded as mature or deliberate, in contradistinction to impulsive volitions, but the difference is not in kind but only in degree of complexity; for in the end, actions conditioned by the resultant of a complex system of associations are of essentially the same character as those conditioned by the simple stimulus of a present feeling or desire, where no other associations have as yet been formed capable of modifying it.

But what is normal in the infant or untutored animal, may be positive insanity on the part of the educated adult. If in him actions are conditioned merely by present feelings or desires, irrespective of, or in spite of, the associations formed by experience between such acts and their consequences as pains, there is a reversion to the infantile type of volition; the only difference being, that in the one case no opposing associations have as yet been formed, while in the other, though formed, they prove of no avail. An individual who so acts, acts irrationally; and if in anyone, notwithstanding the opposing influence of past associations, a present feeling or desire reaches such a pitch of intensity as to overbalance these associations, the individual is said to act in spite of himself, or, metaphorically, against his will. Such tendencies occur more or less in all, but they are exemplified more especially in certain forms of insanity, in which the individual becomes the victim of some morbid desire, and is impelled irresistibly, and to his horror, to commit some act fraught with dreadful consequences.

§ 102. The tendency of feelings or desires to expend themselves in action leads to the consideration of another faculty which plays an important part in the regulation and control of ideation and action.

The primordial elements of the volitional acts of the infant, and also of the adult, are capable of being reduced in ultimate physiological analysis to reaction between the centres of sensation and those of motion.

But besides the power to act in response to feelings or desires, there is also the power to inhibit or restrain action, notwithstanding the tendency of feelings or desires to manifest themselves in active motor outbursts.

Inhibition of action is either direct or indirect.

As an example of indirect inhibition, we may take the inhibition of reflex action, which is caused by a simultaneous stronger sensory stimulus. This is paralleled in volitional action by the inhibition or neutralisation of one motive by another and stronger.

As an example of direct inhibition, we may take the inhibitory action of the vagus upon the heart. This is due to an influence of the vagus on the cardiac motor ganglia by which their activity is restrained. 'The heart contains within itself numerous ganglia, which keep up its rhythmical contractions even for some time after it has been removed from the body. The terminal branches of the vagus nerve in the heart are connected in some way with these ganglia, and whenever it is irritated the ganglia cease to act on the muscular substance, and the heart stands completely still in a relaxed condition. The branches of the vagus which have this action resemble motor nerves in their conveying an irritation applied to them towards the periphery, and not towards the centre, and also in their origin, for although they run in the vagus they are really derived from the spinal accessory nerve, and only join the vagus near its origin. The other fibres of the spinal accessory go to muscles, and when they are excited they set the muscles in action, but those going to the heart do not end in the muscular fibres but in the ganglia, and they produce rest instead of motion, relaxation instead of contraction.' (Lauder-Brunton, 'On Inhibition, Peripheral and Central,' 'West Riding Lunatic Asylum Medical Reports,' vol. iv. p. 181.) The centres of direct inhibition are thus truly motor in character, but their action is expended in the motor centres proper.

As an illustration of volitional inhibition we may take the power, accompanied with the feeling of effort, to rein in and inhibit the tendency of powerful feelings to exhibit themselves in action. The battle between inhibition and the tendency to active motor outburst, is indicated by the tension into which the muscles are thrown, and yet kept reined in, so that under a comparatively calm exterior there may be a raging fire, threatening to burst all bonds.

The inhibitory centres are not equally developed or educated in all, nor are they equally developed in the same individual in respect to particular tendencies to action. But this faculty of inhibition appears to me to be a fundamental element in the attentive concentration of consciousness and control of ideation.

It has been properly remarked that we have no direct volitional control over the centres of ideation. Ideas once excited centrally or from peripherical impressions tend to excite each other in a purely reflex manner, as Laycock and Carpenter have pointed out. Left to themselves ideas excite ideas along the lines of association of contiguity and similarity—coherently in the waking state, when all the centres and senses are functionally active; incoherently in dreams and delirium, where the various centres are functioning irregularly.

But we have the power of concentrating attention on one idea, or class of ideas, and their immediate associates, to the exclusion of all others, a power differently developed in different individuals. We can thus modify and control the current of ideation, and we can also, to a certain extent, voluntarily call up and retain in consciousness particular ideas and particular associations of ideas.

On what physiological basis this psychological faculty rests is an extremely difficult question, and is one scarcely capable of experimental determination. The following considerations are therefore more properly speculations than deductions from experimental data.

§ 103. Both the voluntary excitation of ideas and the concentration of consciousness by which the current of ideation is controlled, seem to be essentially dependent on the motor centres. The fact that attention involves the activity of the motor powers has been clearly enunciated by Bain and Wundt.[1]

Bain ('The Emotions and the Will,' 3rd ed. 1875) remarks as follows:—'It is not obvious at first sight that the retention of an idea in the mind is operated by voluntary muscles. Which movements are operating when I am cogitating a circle, or recollecting St. Paul's? There can be no answer given to this,

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[1] 'Irgend eine vorhandene centrale Sinnesreizung ruft andere hervor, die ihr verwandt sind, oder mit denen sie oft verbunden gewesen ist. Aber die Vorstellungen die so in das allgemeine Blickfeld des Bewusstseins treten, sind zunächst ausserordentlich schwach, bis die Spannung der Aufmerksamkeit hinzukommt, die auf eine oder einige wenige sich concentrirt und dieselben in den Blickpunkt hebt. Diese Wirkung müssen wir uns ganz ebenso wie bei der Apperception der aüsseren Sinneseindrücke denken. Sie besteht in einer willkürlichen Innervation, welche in ihren stärkeren Graden auch hier deutlich als Spannungsgefühl sich verräth. Sie wirkt zurück auf die Sinnescentren und verstärkt so unter allen den leise anklingenden Erregungen eine bestimme, die sich nun als deutliches Errinerungsbild in den Mittelpunkt des Bewusstseins stellt. Wir empfinden diese Spannung der Aufmerksamkeit immer dann als eine willkürliche Thätigkeit, wenn dieselbe zu bedeutenderer Stärke anwachsen muss, um eine bestimmte Vorstellung in den Vordergrund zu ziehen.' ('Physiologische Psychologie,' p. 793.)

unless on the assumption that the mental or revived image occupies the same place in the brain and other parts of the system, as the original sensation did, a position supported by a number of reasons adduced in my former volume ('Contiguity,' § 10). Now there being a muscular element in our sensations, especially of the higher senses—touch, hearing, sight—this element must somehow or other have a place in the after remembrance of the idea.

'The ideal circle is a restoring of those currents that would prompt the sweep of the eye round an ideal circle; the difference lies in the last stage, or in stopping short of the actual movement performed by the organ' (p. 370).

In these sentences, and particularly the last, Bain seems to me to have clearly indicated the elements of attention, which I conceive to be a combination of the activity of the motor, and of the inhibitory-motor centres.

In calling up an idea, or when engaged in the attentive consideration of some idea or ideas, we are in reality throwing into action, but in an inhibited or suppressed manner, the movements with which the sensory factors of ideation are associated in organic cohesion.

We think of form by initiating and then inhibiting the movements of the eyes or hands through which and by which ideas of form have been gained and persist. And just as sensory impressions or sensory ideas tend by association to call up ideal or actual movements, so conversely, the excitation of movements tends to call up by association the various sensory factors which combine with these particular movements to form complex ideas. In the case of ideas, the motor element of which is not apparent, the method of excitation can be referred to the articulatory movements with which as symbols ideas are associated. This is, in fact, the most usual method of recalling ideas in general. We recall an object in idea by pronouncing the name in a suppressed manner. We think, therefore, and direct the current of thought in a great measure by means of internal speech.

This is essentially the case with respect to the recalling of abstract ideas as contradistinguished from concrete and particular.

The abstract qualities and relations of objects exist only by reason of words, and we think of the concrete or particular instances out of which the general or abstract have been formed, by making the symbolic movements of articulation with which these ideas cohere.

An aphasic individual is incapable of abstract ideation or trains of thought. He thinks only in particulars, and his thoughts are conditioned mainly by present impressions on his organs of sense, arousing ideas according to the usual laws of association.

The recall of an idea being thus apparently dependent on excitation of the motor element of its composition, the power of fixing the attention and concentrating consciousness depends, further, on inhibition of the movement.

During the time we are engaged in attentive ideation we suppress actual movements, but keep up in a state of greater or less tension the centres of the movement or movements with which the various sensory factors of ideation cohere.

By checking the tendency to outward diffusion in actual motion, we thereby increase the internal diffusion, and concentrate consciousness. For the degree of consciousness is inversely proportional to the amount of external diffusion in action. In the deepest attention, every movement which would diminish internal diffusion is likewise inhibited. Hence, in deep thought, even automatic actions are inhibited, and a man who becomes deep in thought while he walks, may be observed to stand still.

The excitation of the motor centres, inhibited from external diffusion, expends its force internally along the lines of organic cohesion, and the various factors which have become organically coherent with any particular movement rise into consciousness. This inhibited excitation of a motor centre may be compared to tugging at a plant with branching roots. The tension causes a vibratile thrill to the remotest radicle. So the tension of the motor centre keeps in a state of conscious thrill the ideational centres organically coherent therewith. The centres of inhibition would therefore form the chief factor in the concentration of consciousness and the control of ideation. They have, however, no self-determining power of activity, but are called into action by the same stimuli which tend to excite actual movement. The centres of inhibition undergo education along with the centres of actual motion during the growth of volition. The education of the centres of inhibition introduces the element of deliberation into volition, for action at the instigation of present feelings is suspended until the various associations which have clustered round any individual act have arisen in consciousness. The resultant of the various associations, the revival of which is conditioned by the present feeling and the concentration of consciousness which it instigates, is the motive which ultimately determines the action.

In proportion to the development and degree of education of the centres of inhibition do acts of volition lose their impulsive character, and acquire the aspect of deliberation. Present impulses or feelings, instead of at once exciting action, as in the infant, stimulate the centres of inhibition simultaneously, and suspend action until, under the influence of attention, the associations engendered by past experience between actions and their pleasurable or painful consequences, near and remote, have arisen in consciousness. If the centres of inhibition, and thereby the faculty of attention, are weak, or present impulses unusually strong, volition is impulsive rather than deliberate.

The centres of inhibition being thus the essential factor of attention, constitute the organic basis of all the higher intellectual faculties. And in proportion to their development we should expect a corresponding intellectual power.

'A great profusion of remembered images, ideas, or notions, avails little for practical ends without the power of arrest or selection, which in its origin is purely voluntary. We may have the luxuriousness of a reverie or a dream, but not the compliance with a plan of operations, or with rules of composition.' (Bain, *op. cit.*, p. 371.)

§ 104. In proportion to the development of the faculty of attention are the intellectual and reflective powers manifested. This is in accordance with the anatomical development of the frontal lobes of the brain, and we have various experimental and pathological data for localising in these the centres of inhibition, the physiological substrata of this psychological faculty.

It has already been shown that electrical irritation of the antero-frontal lobes causes no motor manifestations, a fact which, though a negative one, is consistent with the view that, though not actually motor, they are inhibitory-motor, and expend their energy in inducing internal changes in the centres of actual motor execution.

Centres of direct inhibition and nerves of inhibition are, as we have seen, all centrifugal, or motor, in character, and it has also been shown that the frontal regions are directly connected with the centrifugal, or motor, tracts of the peduncular expansion or corona radiata.

The removal of the frontal lobes causes no motor paralysis, or other evident physiological effects, but causes a form of mental degradation, which may be reduced in ultimate analysis to loss of the faculty of attention.

The powers of attention and concentration of thought are, further, small and imperfect in idiots with defective development of the frontal lobes, and disease of the frontal lobes is more especially characteristic of dementia or general mental degradation. The frontal regions which correspond to the non-excitable regions of the brain of the monkey are small or rudimentary in the lower animals, and their intelligence and powers of reflective thought correspond.

The development of the frontal lobes is greatest in man with the highest intellectual powers, and taking one man with another, the greatest intellectual power is characteristic of the one with the greatest frontal development.

The phrenologists have, I think, good grounds for localising the reflective faculties in the frontal regions of the brain, and there is nothing inherently improbable in the view that frontal development in special regions may be indicative of the power of concentration of thought and intellectual capacity in special directions.

§ 105. In this chapter I have contented myself with indicating very briefly some of the more important psychological principles which seem to me fairly deducible from experimental investigation into the anatomical and physiological substrata of mind, principles which in many respects coincide with those expounded by Bain and Herbert Spencer.

Many other important points in cerebral physiology still remain to be considered, such as the relation of the encephalic centres to nutritive or trophic processes; the conditions of the normal activity of the brain; the physiological conditions of consciousness etc.; but as these questions require discussion in the light more of the phenomena of disease in man, than of experiments on the lower animals, I propose to reserve these and similar topics for another treatise, specially devoted to the consideration of diseases of the brain.

CHAPTER XII.

DIAGRAMMATIC SUMMARY.

§ 106. In the following diagram and system of nomenclature, I have endeavoured to represent, in a summary and schematic manner, the mutual relations of the spinal and encephalic centres discussed at length in the preceding chapters.

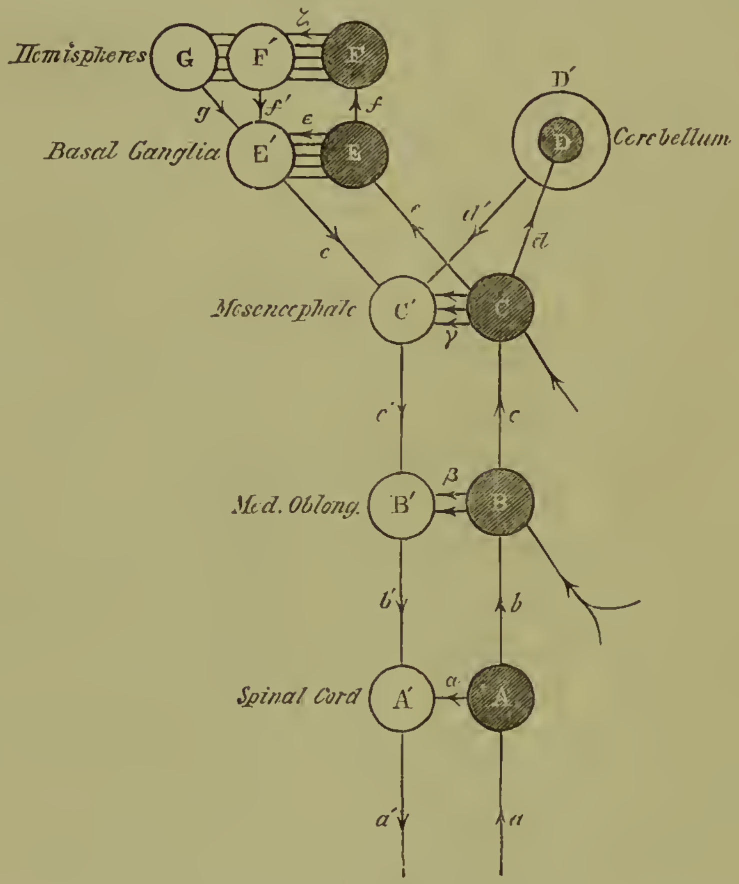

Fig. 58.—Schematic Diagram of the Cerebro-spinal Nerve-centres. The further explanation of the diagram is given in the text.

The *Spinal Centres* are indicated in the figure (fig. 58), by the circles (A) (A′); the one (A) representing the sensory or afferent, the other (A′), the motor or efferent divisions, joined by the intra central communication *a*.

The afferent nerve or nerves leading to (A) are indicated by *a*, the direction of the arrow indicating the centripetal character of the fibres in this as in the higher regions. The other line *a′* is the centrifugal or motor nerve. An impression *a* causes the action *a′* in a *reflex* or *excito-motor* manner, quite independently of the higher centres. Hence, all the parts of the cerebro-spinal system above A A′ may be removed without destroying reflex action (see Chap. II.).

In order to carry out a uniform system of nomenclature, we may designate this independent activity of the spinal centres by the term *kentro-kinetic*, which is simply the Greek equivalent of excito-motor, (*κέντρον* = spur; *κινέω* = I move.)

Medulla Oblongata.

§ 107. The centres of the medulla oblongata are represented by the circles (B) (B′), of which (B) is the sensory, and (B′) the motor division. The independent functional activity of the medulla oblongata is of greater complexity than that of the spinal cord, but of essentially the same nature, *viz.*, reflex or excito-motor.

On account of the greater complexity and multiplicity of sensory and motor co-ordinations in the medulla oblongata, the medullary centres may be described as the regions of compound reflex action—*syn-kentro-kinesis* or *syn-kentro-kinetic* action.

It may be seen by the diagram that the impression *a*, which in the spinal centres (A) (A′) causes the action *a′*, carried to the medulla as *b*, may produce through (B) *β* (B′) and *b′*, precisely the same muscular action *a′*, but as part of a higher and special co-ordination. The special forms of co-ordinated reflex actions exhibited by the medulla oblongata have been described in Chap. III.

In the same manner as the reflex functions of the spinal cord may continue after removal of all above (A) (A′), so the compound reflex actions of the medulla oblongata may continue to be performed after removal of all the centres situated above (B) (B′).

The diagram also shows graphically that section below (A) (A′), or between (A) (A′) and (B) (B′), must cause paralysis of the functional manifestations of the centres situated higher up, in so far as they are concerned with a and a'.

Mesencephalic Centres.

§ 108. The mesencephalic centres, as has been shown in Chap. IV., are the centres of co-ordination of still more complex forms of activity, such as of locomotion, emotional expression, etc., more especially elicited in response to impressions made on the organs of special sense. The forms of activity manifested by these centres are usually termed consensual or sensori-motor (Carpenter). On account of the ambiguity involved in the employment of the term sensori-motor, and inasmuch as sensation in the psychological acceptation of the term, *viz.*, consciousness of sensory impressions, cannot be predicated of these centres, I would employ the term *æsthetiko-kinetic*, to signify the activity of the mesencephalic ganglia, arbitrarily defining æsthesis as a physical, in contradistinction to a psychical, modification of special sensory nerve centres.

In so far as the action a' is part of the manifestation of the functional activity of the mesencephalic centres, it is the result of æsthetiko-kinesis, while the same action, conditioned by the spinal or medullary centres, is kentro-kinetic, or syn-kentro-kinetic respectively.

The signification of the action differs according to the centre by which it is conditioned.

It is further shown by the diagram that all above the centres (C) (C′) may be removed without destroying æsthetiko-kinetic action; but, as I have endeavoured to show, the development of these centres and degree of independence which they possess are inversely proportional to the development of the cerebral hemispheres. Hence, in different animals the effects of removal of the cerebral hemispheres vary, in accordance with this law. It is also obvious that the paths of æsthetiko-kinesis are not independent of those concerned in kentro-, or syn-kentro-kinesis, and therefore a lesion which destroys the centres, or paths, of these forms of activity must, *ipso facto*, paralyse the manifestation of æsthetiko-kinetic action.

Cerebellum.

§ 109. The sensory (D) and the motor (D′) centres are represented in the diagram as included the one within the other, the two not having been definitely anatomically differentiated from each other. The sensory and motor relations of the cerebellum are indicated by the arrows *d* and *d′* respectively.

The activity of the cerebellum, as I have endeavoured to show in Chap. VI., is simply a branch or division of æsthetikokinesis, and is intimately bound up with the activity of the mesencephalic centres, though capable to some extent of complete differentiation. The æsthetiko-kinetic action of the cerebellum specially relates to the function of equilibration, or *isorropesis* (equilibration).

The diagram shows how the centres and paths concerned in this form of activity may be removed without destroying the functional manifestations of the mesencephalic ganglia, or of the cerebral hemispheres proper.

The action *a′* therefore, in so far as it is concerned in the function of equilibration, becomes paralysed, *quà* this function only, by destruction of (D) (D′) or *d d′*.

Its excitation from the cerebral hemispheres in volition, or its excitation reflexly through the spinal centres, is left intact. So, also, section of the afferent fibres going to the cerebellar centres does not necessarily impede the transmission of sensory impressions to the centres of consciousness. The diagram, therefore, shows that neither sensation nor voluntary motion need be affected by disease of the cerebellum.

All above (C) (C′) and (D) (D′) may be removed by section through the tracts (E) (E′), which correspond to the crura cerebri, without destroying the functions of equilibration, co-ordinated locomotion, etc., facts experimentally demonstrated in the lower animals, in which the mesencephalic centres reach a high development in comparison with the cerebral hemispheres.

The Basal Ganglia.

§ 110. The optic thalami and the corpora striata are represented in the diagram by (E) and (E′) respectively, and their connections with the sensory and motor tracts of the crus by *e* and *e′* respectively. The intra-central connections are indicated by the parallel lines (ε).

The basal ganglia, as has been argued in Chap. X., are the centres of a form of activity, subordinate to that of the hemispheres proper, frequently termed secondary-reflex or automatic action. The various sensory and motor centres which are differentiated in the hemispheres are integrated in these ganglia, and organic nexuses may be established between them, so that actions at first requiring volitional education and conscious exertion become organised, as it were, reflexly or automatically in these ganglia. As their functional activity is below the domain of consciousness, these ganglia may be termed the centres of *hypo-noetiko-kinetic* action, a term which indicates their subordination to the hemispheres, the action of which I propose to call *noetiko-kinetic* (see below).

It is obvious from the diagram, that destruction of the centres (E) (E′) cuts off all communication between the hemispheres and the sensory and motor tracts, and necessarily therefore, besides destroying hypo-noetiko-kinetic action, destroys true sensation and voluntary motion, functions belonging only to the hemispheres.

The Cerebral Hemispheres.

§ 111. The sensory regions of the hemispheres are represented in the diagram by (F), and the motor by (F′), while ζ indicates the associating fibres between the sensory and motor centres. By (G) are indicated the frontal regions, the centres, as has been argued (XI., § 104), of inhibition, or inhibitory-motor centres.

The respective communications between these centres and the basal ganglia are represented by the arrows *f*, *f′*, *g*, the direction of the arrow indicating the centripetal or centrifugal direction.

The reaction between the sensory and motor centres (F) (F′) involves consciousness, which we may call noesis, and therefore we may designate the activity of the hemispheres by the term *noetiko-kinetic.* The term noetiko-kinetic may be further differentiated into *ana-noetiko-kinetic*, indicating actions conditioned by revived or ideal impressions; and the results of compound associations may be termed *syn-noetiko-kinetic* actions, etc.

But noetiko-kinesis is under the control of the centres (G), which, as being the basis of attention, may be termed the centres of *kata-noesis* or *kata-noetiko-kinetic action*.

Though the various spinal and encephalic centres have thus their own special modes of activity, capable, more or less, of individual and independent separation, yet they form only parts of a complex whole, not acting disconnectedly or out of relation to each other, but all more or less engaged in the most ordinary and apparently most simple forms of functional manifestation.

CHAPTER XIII.

CEREBRAL AND CRANIAL TOPOGRAPHY.

§ 112. In the foregoing chapters, numerous clinical and pathological facts have been adduced, tending to establish the physiological homology of the brain of man with that of the ape, both generally and in respect to individual anatomically homologous parts.

The object of this chapter is to trace these anatomical and physiological homologies in greater detail, and to indicate the relations which subsist between the cerebral convolutions and the surface of the cranium.

In addition to the pathological evidence of the existence of differentiated motor centres in the human brain, supplied by the observations of Hughlings-Jackson and others, we have experimental confirmation of the same in the investigations of Dr. Bartholow (' Experimental Investigations into the Functions of the Human Brain,' 'Amer. Journ. of the Med. Sciences,' April 1874), who ventured to apply the electric stimulus directly to the surface of the brain, in the case of a patient whose brain was more or less exposed by cancerous ulceration of the skull. As this procedure is fraught with danger to life, it is not to be commended, or likely to be repeated. Dr. Bartholow found that the insertion of needle electrodes, in connection with an induction coil, into the grey matter of the hemisphere in the region of the postero-parietal lobe (fig. 59, P_1), caused convulsive movements of the opposite arm and leg, facts which bear out the results of electrical irritation of this region in the brain of the monkey (fig. 64, 1), which, as has been shown (Chap. VIII.), causes movements of the opposite leg and foot. The results obtained by Dr. Bartholow were, however, of a more complex nature, owing to the method and the state of the patient not being consistent with the conditions of exact localisation of the stimulus. The great fact, however, is the experimental demonstration that irritation of the cortex cerebri in man, in regions corresponding anatomically to the motor centres in the brain of the monkey, also gives rise to movements on the opposite side of the body.

§ 113. The brain of man is constructed on the same type as that of the monkey, and essentially the same primary fissures and convolutions are recognisable in both, the chief differences consisting in the greater complexity of the convolutional arrangement of the human brain, caused by the development of numerous secondary and tertiary gyri, which tend to obscure the simple type of the simian brain. These differences are more marked in the adult and highly developed brain, but are less pronounced in the fœtal human brain.

The topography, homologies and nomenclature of the cerebral convolutions have been investigated and established more especially by Gratiolet, Bischoff, Huxley, Turner, Ecker, etc. The nomenclature is not altogether uniform. In the following description I have principally followed that of Ecker ('The Convolutions of the Human Brain,' translated by Galton), which, with certain differences, which are indicated, agrees in the main with that of Huxley, Turner, and English anatomists and pathologists.

§ 114. Of the primary fissures or sulci the fissure of Sylvius (fig. 59, S) is easily recognised, and the corresponding fissure, (fig. 60, A) in the brain of the monkey evident. The fissure of Sylvius divides into two rami, the posterior or horizontal (S′) and the ascending or anterior (S″). The portion included between these two branches sometimes receives the name of the *Operculum* (klappdeckel), and forms the roof of the island of Reil. The *Fissure of Rolando* (C) or *Central Sulcus*, corresponds in position and direction with B (fig. 60) in the brain of the monkey.

The *Parieto-occipital Fissure* (fig. 59, *po*) corresponds to C (fig. 60) in the brain of the monkey.

§ 115. *The Frontal Lobe* (fig. 59, F), including the region situated in advance of the fissure of Rolando (C), is divided by secondary fissures into the following convolutions :—F_1, the

Superior Frontal Convolution; F_2, the *Middle Frontal Convolution*; F_3, the *Inferior* or *Third Frontal Convolution.*

The sulci, which separate these convolutions from each other, are termed respectively the *Supero-Frontal* (fig. 59, f_1) and *Infero-Frontal* (f_2). (Compare *sf* and *if*, fig. 60).

FIG. 59.—Lateral View of the Human Brain (Ecker). F. Frontal lobe. P. Parietal lobe. O. Occipital lobe. T. Temporo-sphenoidal lobe. S. Fissure of Sylvius. S′ Horizontal, S″ Ascending ramus of the same. *c.* Sulcus centralis, or fissure of Rolando. A. Anterior central convolution, or ascending frontal. B. Posterior central convolution, or ascending parietal. F_1 Superior; F_2 Middle; F_3 Inferior frontal convolutions. f_1 Superior, f_2 Inferior frontal sulcus; f_3 Sulcus præcentralis. P_1 Superior parietal lobule, or postero-parietal lobule; P_2 Inferior parietal lobule, viz. P_2 Gyrus supra-marginalis; P_2' Gyrus angularis. *ip.* Sulcus intraparietalis. *cm.* Termination of the calloso-marginal fissure. O_1 First, O_2 Second, O_3 Third occipital convolutions. *po.* Parieto-occipital fissure. *o.* Sulcus occipitalis transversus; o_2, Sulcus occipitalis longitudinalis inferior. T_1 First, T_2 Second, T_3 Third temporo-sphenoidal convolutions. t_1 First, t_2 Second temporo-sphenoidal fissures.

The three frontal convolutions terminate posteriorly in a convolution which forms the anterior boundary of the fissure of Rolando, termed the *Anterior Central*, *Ascending Frontal* (Turner), or *Antero-parietal Convolution* (Huxley) (fig. 59, A).

The continuity of the three frontal convolutions with the ascending frontal is interrupted by a sulcus termed the *Antero-parietal Sulcus* (Huxley), or *Sulcus Præcentralis* (Ecker) (fig. 59, f_3) corresponding to *ap* (fig. 60) in the brain of the monkey. The ascending ramus of the fissure of Sylvius (s'') likewise interrupts the continuity of the inferior frontal convolution with the ascending frontal. This ramus is regarded by Turner as the continuation of the antero-parietal sulcus; but this, according to Ecker, is a quite exceptional occurrence. The position of the ascending ramus of the fissure of Sylvius may perhaps be indicated in the brain of the monkey, by a slight depression situated at the lower extremity of the ascending frontal gyrus (fig. 60).

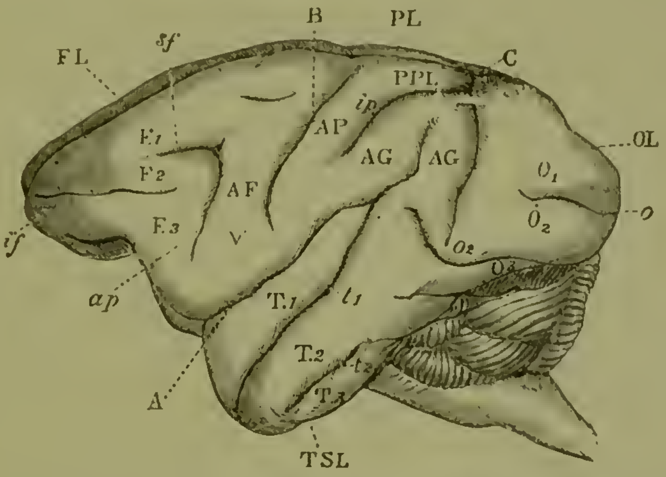

FIG. 60.—Left Hemisphere of the Brain of the Monkey. (Macacque). A. The fissure of Sylvius. B. The fissure of Rolando. C. The parieto-occipital fissure. FL. The frontal lobe. PL. The parietal lobe. OL. The occipital lobe. TSL. The temporo-sphenoidal lobe. F_1. The superior frontal convolution. F_2. The middle frontal convolution. F_3. The inferior frontal convolution. *sf*. The supero-frontal sulcus. *if*. The infero-frontal sulcus. *ap*. The antero-parietal sulcus. AF. The ascending frontal convolution. AP. The ascending parietal convolution. PPL. The postero-parietal lobule. AG. The angular gyrus. *ip*. The intra-parietal sulcus. T_1, T_2, T_3. The superior, middle, and inferior temporo-sphenoidal convolutions. t_1, t_2. The superior and inferior temporo-sphenoidal sulci. O_1, O_2, and O_3. The superior, middle, and inferior occipital convolutions. o, o_2. The first and second occipital fissures.

The inferior aspect of the frontal lobe is sometimes termed the orbital lobule, from its position in reference to the roof of the orbit (see fig. 7, 2′, fig. 62, F O).

§ 116. *The Parietal Lobe* (fig. 59, P) is bounded in front by the fissure of Rolando, behind by the *Parieto-Occipital Fissure* (fig. 59, *p o*), and is separated from the temporo-sphenoidal lobe by the horizontal ramus of the fissure of Sylvius (fig. 59, s′).

In this lobe several convolutions are differentiated. The first, which forms the posterior boundary of the fissure of Rolando, is termed the *Ascending Parietal Convolution* (Turner), *Postero-Parietal Gyrus* (Huxley), or *Posterior Central Convolution* (Ecker) (fig. 59, B), corresponding to A P, fig. 60, in the brain of the monkey. This convolution is bounded posteriorly by a sulcus termed the *Intra-Parietal Sulcus* (fig. 59, *i p*, and also fig. 60).

The part above the posterior extremity of the intra-parietal sulcus, and between it and the longitudinal fissure, is sometimes termed the *Superior Parietal Lobule* (Ecker); by Huxley and Turner it is termed the *Postero-Parietal Lobule*, and is the superior posterior termination of the ascending parietal convolution (fig. 59, P_1), corresponding to P P L, fig. 60, in the brain of the monkey. This lobule is bounded posteriorly by the parieto-occipital fissure, which separates it from the occipital lobe.

Below the intra-parietal fissure are situated a group of convolutions arching over the upper extremities of the Sylvian fissure, and the superior temporo-sphenoidal fissure (fig. 59, t_1) more complex and less distinctly marked off from each other than in the brain of the monkey. This region is termed the *Inferior Parietal Lobule* (Ecker), and consists of an anterior division, arching over the upper end of the fissure of Sylvius, termed the *Supra-Marginal Lobule*, or *Lobule du Pli Courbe* (Gratiolet) (fig. 59, P_2); and a posterior division, which arches over the upper end of the superior temporo-sphenoidal fissure, and becomes continuous with the middle temporo-sphenoidal convolution (fig. 59, T_2) and is termed the *Pli Courbe* (Gratiolet), or the *Angular Gyrus* (Huxley) (fig. 59, P_2'). In the monkey —macacque, there is no clear differentiation of this region into a supra-marginal lobule, and an angular gyrus. The two are represented together in fig. 60, A G, the anterior inferior part of which may be regarded as the homologue of the highly-developed supra-marginal lobule in the human brain.

§ 117. *The Temporo-Sphenoidal Lobe* (fig. 59, T) lies behind and below the fissure of Sylvius, which separates it from the frontal and parietal lobes; posteriorly it merges with the occipital lobe, the anterior boundary of which is formed by the parieto-occipital fissure.

The temporo-sphenoidal lobe is divided by two sulci into three tiers of convolutions. One fissure which runs parallel to the horizontal ramus of the fissure of Sylvius, is termed the *Superior Temporo-Sphenoidal Fissure* (fig. 59, t_1), or *Parallel Fissure* (Gratiolet). Between the fissure of Sylvius and the superior temporo-sphenoidal fissure lies the *Superior Temporo-Sphenoidal Convolution* (fig. 59, T_1), or, as it is sometimes termed, the *Infra-Marginal Gyrus.*

Another fissure, running parallel to the superior temporo-sphenoidal fissure, is termed the *Middle Temporo-Sphenoidal Fissure* (fig. 59, t_2). Between these two is situated the *Middle Temporo-Sphenoidal Convolution* (fig. 59, T_2).

On the inferior aspect of this lobe is another fissure termed the *Inferior Temporo-Sphenoidal Fissure*, which forms the lower boundary of the *Inferior Temporo-Sphenoidal Convolution* (fig. 59, T_3). The corresponding regions in the brain of the monkey are indicated by the same letters (fig. 60).

§ 118. *The Occipital Lobe* (fig. 59, O) is not defined anteriorly, except at the site of the parieto-occipital fissure. It fuses with the parietal and temporo-sphenoidal lobes by means of connecting gyri, termed by Gratiolet 'bridging convolutions,' or 'plis de passage.'

Ecker objects to the use of the term 'bridging convolutions,' and gives special names to the convolutions on the lateral aspect of the occipital lobe, as follows:—The *Gyrus Occipitalis Primus* (fig. 59, O_1) connects the occipital lobe with the postero-parietal lobule. It is termed by Gratiolet the *Pli de Passage Supérieur Externe*, and *Pli Occipital Supérieur*, and by Huxley, the *First External Annectent Gyrus.* This convolution is separated from the next by a sulcus termed the *Sulcus Occipitalis Transversus* (fig. 59, o) corresponding to (o), fig. 60, in the brain of the monkey. The next convolution is termed the second occipital, or *Gyrus Occipitalis Secundus* (O_2, figs. 59 and 60), or *Deuxième Pli de Passage Externe* (Gratiolet), or *Second External Annectent Gyrus* (Huxley). This convolution runs anteriorly into the gyrus angularis. The third occipital convolution, or *Gyrus Occipitalis Tertius* (fig. 59, O_3) runs parallel with the preceding, and joins the third temporo-sphenoidal convolution anteriorly. It is termed by Gratiolet the *Troisième et Quatrième Pli de Passage Externe*, or *Pli Occipital Inférieur.*

§ 119. On the internal or mesial aspect of the hemisphere, the following fissures and convolutions are differentiated.

The convolution immediately bounding the corpus callosum (fig. 61, C C) is termed the *Gyrus Fornicatus* (G *f*). It commences at the frontal extremity of the brain, beneath the anterior extremity, or *genu*, of the corpus callosum, and terminates posteriorly in the *Gyrus Uncinatus*, or *Uncinate Gyrus* (fig. 61, H), or *Gyrus Hippocampi.* The gyrus uncinatus ends anteriorly in a crook-like extremity, or crochet, *Uncus Gyri Fornicati*, or *Subiculum Cornu Ammonis* (fig. 61, U), (fig. 62, S)

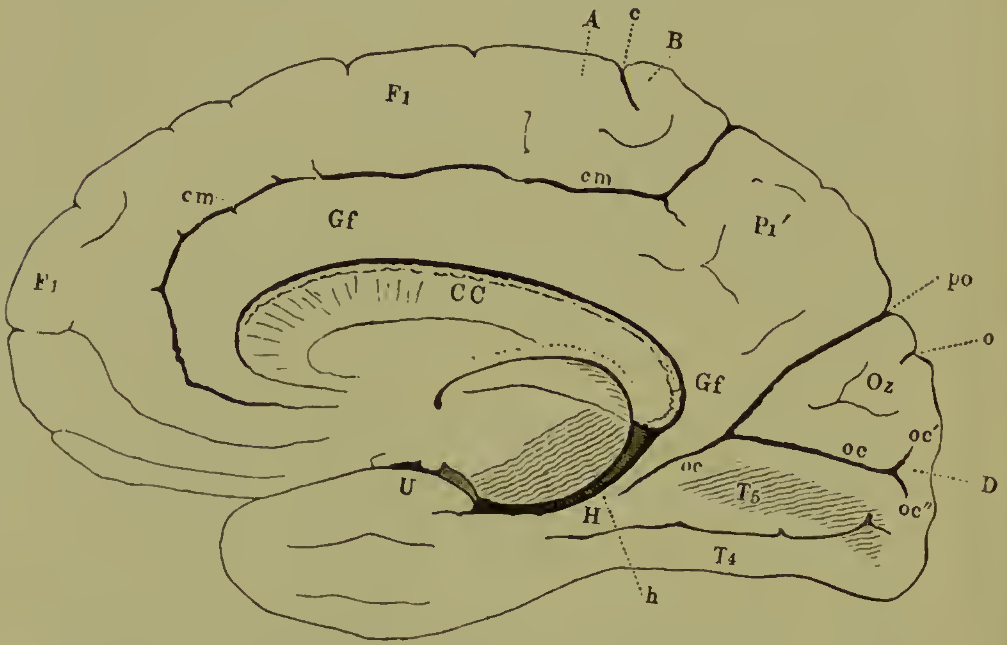

FIG. 61.—View of the Median Aspect of the Right Hemisphere of the Human Brain. (Ecker). CC. Corpus callosum, longitudinally divided. G*f*. Gyrus fornicatus. H. Gyrus hippocampi. *h*. Sulcus hippocampi. U. Uncinate gyrus. *cm*. Sulcus calloso-marginalis. F_1. Median aspect of the first frontal convolution. *c*. Terminal portion of the sulcus centralis, or fissure of Rolando. A. Anterior; B. Posterior central convolution. P′. Præcuneus. Oz. Cuneus. *po*. Parieto-occipital fissure. *o*. Sulcus occipitalis transversus. *oc*. Calcarine fissure. *oc*′. Superior; *oc*″. Inferior ramus of the same. D. Gyrus descendens. T_4. Gyrus occipito-temporalis lateralis (lobulus fusiformis). T_5. Gyrus occipito-temporalis medialis (lobulus lingualis).

Above the gyrus fornicatus, and separated from it by a fissure termed the *Calloso-Marginal Fissure* (fig. 61, *c m*) is a convolution which forms the internal margin of the longitudinal fissure, and has received the name of the *Marginal Convolution* (fig. 61, F$_1$). It is merely the mesial or internal aspect of the convolutions of the frontal and parietal lobes.

Between the posterior extremity of the calloso-marginal sulcus and the parieto-occipital fissure (fig. 61, *p o*) is a lobule of a quadrilateral form, which is the mesial aspect of the postero-parietal lobule. This is termed the *Quadrilateral Lobule*, or *Præcuneus* (fig. 61, P$_1$). Inferiorly, it is continuous with the gyrus fornicatus. A similar disposition is recognisable in the brain of the monkey (fig. 62, Q).

The fissure *o c* (fig. 61), termed the *Calcarine Fissure*, marks the position internally of the calcar avis, or hippocampus

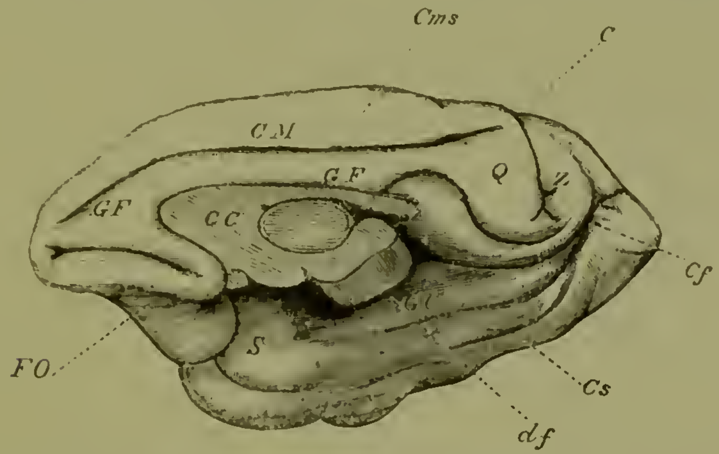

FIG. 62.—The Internal Aspect of the Right Hemisphere of the Monkey (Macacque). CC. The corpus callosum divided. C. The internal parieto-occipital fissure. *cms.* The calloso-marginal fissure. *Cf.* The calcarine fissure. *df.* The dentate fissure. *Cs.* The collateral fissure. GF. The gyrus fornicatus. CM. The marginal convolution. GU. The uncinate convolution. S. The crochet, or subiculum cornu Ammonis. Q. The quadrilateral lobule, or præcuneus. Z. The cuneus. FO. The orbital lobule.

minor, in the posterior cornu of the lateral ventricle. The parieto-occipital fissure is seen to fuse with this at an acute angle. The calcarine fissure is not, as in the monkey (fig. 62, *Cf*), continued anteriorly into the *Dentate Fissure* (fig. 61, *h*), or *Sulcus Hippocampi*, and, therefore, does not completely interrupt the continuity of the gyrus fornicatus with the gyrus uncinatus. The dentate fissure marks the position of the hippocampus major, or cornu Ammonis, in the descending cornu of the lateral ventricle. In this fissure the *Fascia Dentata*, *Corps godronné*, or *dentate gyrus*, which forms a border to the hippocampus major, is situated.

Between the parieto-occipital and calcarine fissures, a wedgeshaped lobule is marked off on the mesial aspect of the occipital lobe. This is termed the *Cuneus* (fig. 61, o *z*), or *Internal Occipital Lobule* (Huxley), (fig. 62, *z*).

Running along the internal or mesial aspect of the occipital and temporo-sphenoidal lobes, is a fissure termed the *Collateral Fissure* (Huxley), or *Sulcus Occipito-Temporalis*, which separates two convolutions from each other, which connect the occipital and temporo-sphenoidal lobes with each other, and are, therefore, termed by Ecker the occipito-temporal convolutions (fig. 62, T_4 and T_5). The upper of these is termed the *Gyrus Occipito-Temporalis Medialis*, or *Lingual Lobule* (fig. 61, T_5). The lower, which frequently merges with the inferior temporo-sphenoidal convolution, but at other times is marked off by a fissure, is termed the *Gyrus Occipito-Temporalis Lateralis*, or *Lobulus Fusiformis* (fig. 61, T_4). A similar disposition is seen

Fig. 63.—Lateral view of the Human Brain. The circles and letters have the same signification as those in the brain of the monkey, fig. 64.

in the brain of the monkey (fig. 62), though the divisions are not so pronounced.

§ 120. Within the lips of the fissure of Sylvius, and concealed by the *Operculum*, or region included between the ascending and horizontal rami of this fissure, lies the central lobe, or island of Reil, which covers the extra-ventricular nucleus of the corpus striatum. Its surface is marked by certain radiating short convolutions, termed the *Gyri Breves* (see fig. 4, c).

§ 121. In the accompanying figures (figs. 63 to 66) I have indicated approximately the situation of the centres or areas homologous with those experimentally determined in the brain of the monkey. An exact correspondence can scarcely be supposed to exist, inasmuch as the movements of the arm and hand are more complex and differentiated than those of the monkey; while, on the other hand, there is nothing in man to correspond with the prehensile movements of the lower limbs and tail in the monkey.

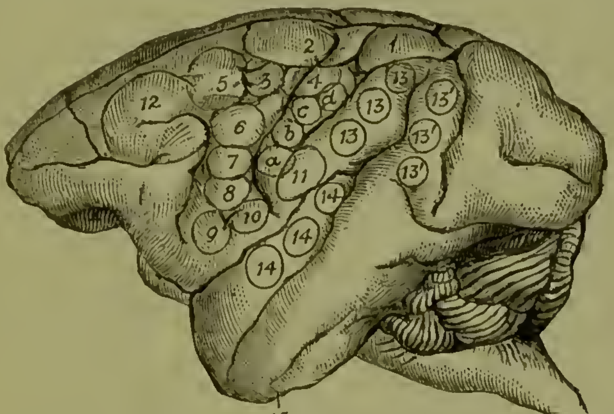

FIG. 64.—The Left Hemisphere of the Monkey (see fig. 29 with description).

In fig. 63 a lateral view of the left hemisphere of the human brain is given, and the same letters placed on regions approximately corresponding to those on fig. 64.

In fig. 65 the upper surface of the human brain is displayed, and the same system followed, to allow of comparison with fig. 66. For the complete details reference is made to chapter VIII., § 53.

(1), placed on the postero-parietal lobule, indicates the position of the centres for movements of the opposite leg and foot such as are concerned in locomotion (*vide* p. 141).

(2), (3), (4), placed together on the convolutions bounding the upper extremity of the fissure of Rolando, include centres for various complex movements of the arms and legs, such as are concerned in climbing, swimming, etc. (*vide* pp. 141-2).

(5), situated at the posterior extremity of the superior frontal convolution, at its junction with the ascending frontal, is the centre for the extension forwards of the arm and hand, as in putting forth the hand to touch something in front (*vide* p. 143).

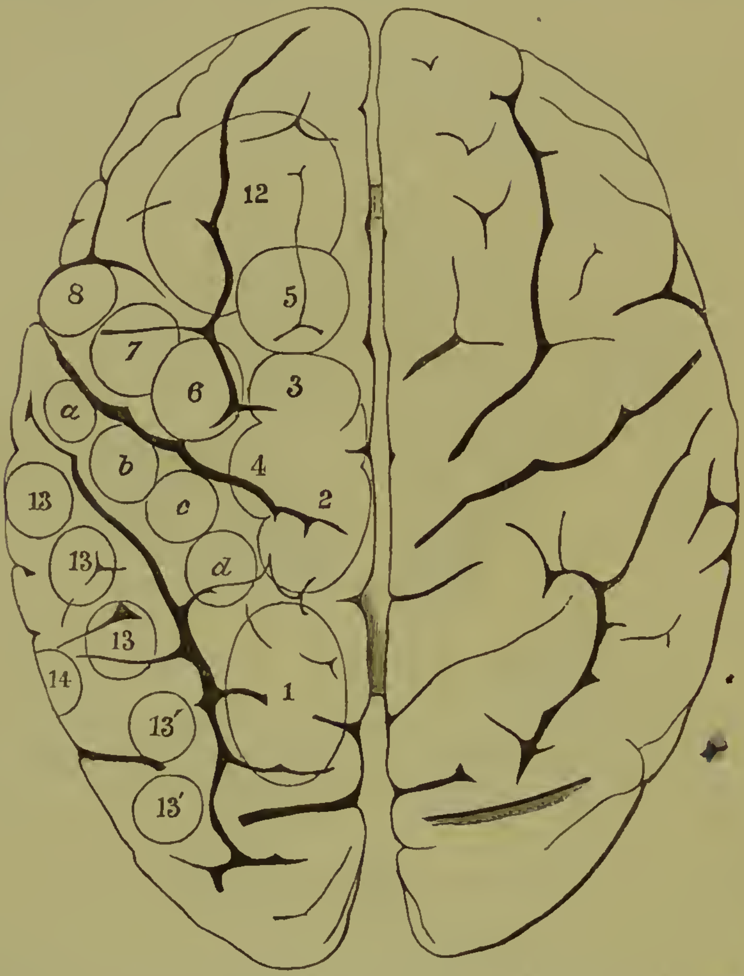

Fig. 65.—Upper Surface of the Human Brain. The circles and letters have the same signification as those on the brain of the Monkey, fig. 66.

(6), situated on the ascending frontal, just behind the upper end of the posterior extremity of the middle frontal convolution, is the centre for the movements of the hand and forearm in which the biceps is particularly engaged, *viz.*, supination of the hand and flexion of the forearm (*vide* pp. 143 and 203).

(7) and (8), centres for the elevators and depressors of the angle of the mouth respectively (*vide* p. 143).

(9) and (10), included together in one, mark the centre for the movements of the lips and tongue, as in articulation. This is the region, disease of which causes aphasia, and is generally known as Broca's convolution (*vide* pp. 143 and 272).

(11), the centre of the platysma, retraction of the angle of the mouth (*vide* p. 143).

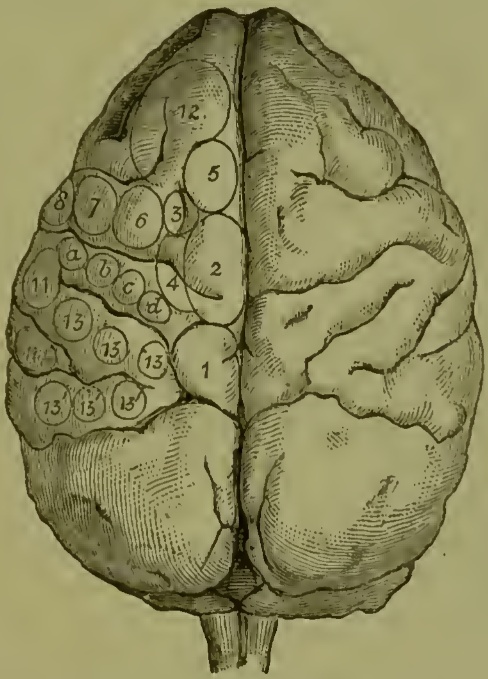

Fig. 66.—Upper Surface of the Hemispheres of the Monkey. The circles and included numerals are explained in connection with fig. 28.

(12), a centre for lateral movements of the head and eyes, with elevation of the eyelids and dilatation of pupil (*vide* pp. 143 and 229).

(*a*), (*b*), (*c*), (*d*), placed on the ascending parietal convolution, indicate the centres of movement of the hand and wrist (*vide* p. 143.)

Circles (13) and (13′) placed on the supra-marginal lobule and angular gyrus, indicate the centre of vision (*vide* p. 144, and Chap. IX., § 65).

Circles (14) placed on the superior temporo-sphenoidal convolution, indicate the situation of the centre of hearing (*vide* p. 144, and Chap. IX. § 66).

The centre of smell is situated in the subiculum cornu Ammonis (fig. 61, U) (*vide* p. 144 and Chap. IX. § 69).

In close proximity, but not exactly defined as to limits, is the centre of taste (*vide* Chap. IX. § 69).

The centre of touch is situated in the hippocampal region (fig. 61, H) (*vide* Chap. IX. § 67).

The functions of the other cerebral regions have been discussed in Chap. IX. § 71, and Chap. XI., § 104.

Relations of the Convolutions to the Skull.

§ 122. The determination of the exact relations of the primary fissures and convolutions of the brain to the surface of the cranium is of importance to the physician and surgeon, as a guide to the localisation and estimation of the effects of diseases and injuries of the brain and its coverings, and may prove of great service in anthropological and craniological investigations.

This subject has been investigated by Broca, Heftler, Féré, Turner, and others by various methods. (For a critical review of the various researches in this direction see a paper by P. Broca, 'La Topographie Cranio-Cérébrale,' 'Revue d'Anthropologie,' 1876. Tome V. No. 2.) The method and rules of determination proposed by Turner ('Journal of Anat. and Phys.,' vols. xiii. and xiv., November 1873 and May 1874) seem to me to be the best adapted for practical purposes. The following account is founded on Turner's investigations:—

'In conducting an investigation of this kind, it is in the first instance necessary to have a clear conception of certain well-defined landmarks, which can be seen or felt when the outer surface of the skull and head are examined. The external occipital protuberance (fig. 67, O), the parietal (P), and frontal (F) eminences, and the external angular process of the frontal bone (A) are easily recognised structures, the position of which can be determined by manipulating the scalp, and still more readily on the surface of the skull itself. The coronal (*c*) and lambdoidal (*l*) sutures can also be felt through the scalp in most heads, and on the skull itself, the position of the squamous (*s*), squamoso-sphenoid (*s s*), and parieto-sphenoid sutures (*p s*), and the curved line of the temporal ridge (*t*), can also without difficulty be determined' (Turner, *op. cit.*) [references inserted].

With these as fixed points, the surface of the skull may be divided into ten well-defined areas or regions.

The coronal suture (*c*) forms the posterior boundary of the *frontal area*. An imaginary line (fig. 67, 2) drawn from the squamous suture (*s*) vertically upwards through the parietal eminence (P) to the sagittal suture or middle line of the skull subdivides the parietal region into an *antero-parietal* (fig. 67, SAP+IAP) and a *post-parietal area* (fig. 67, SPP + IPP).

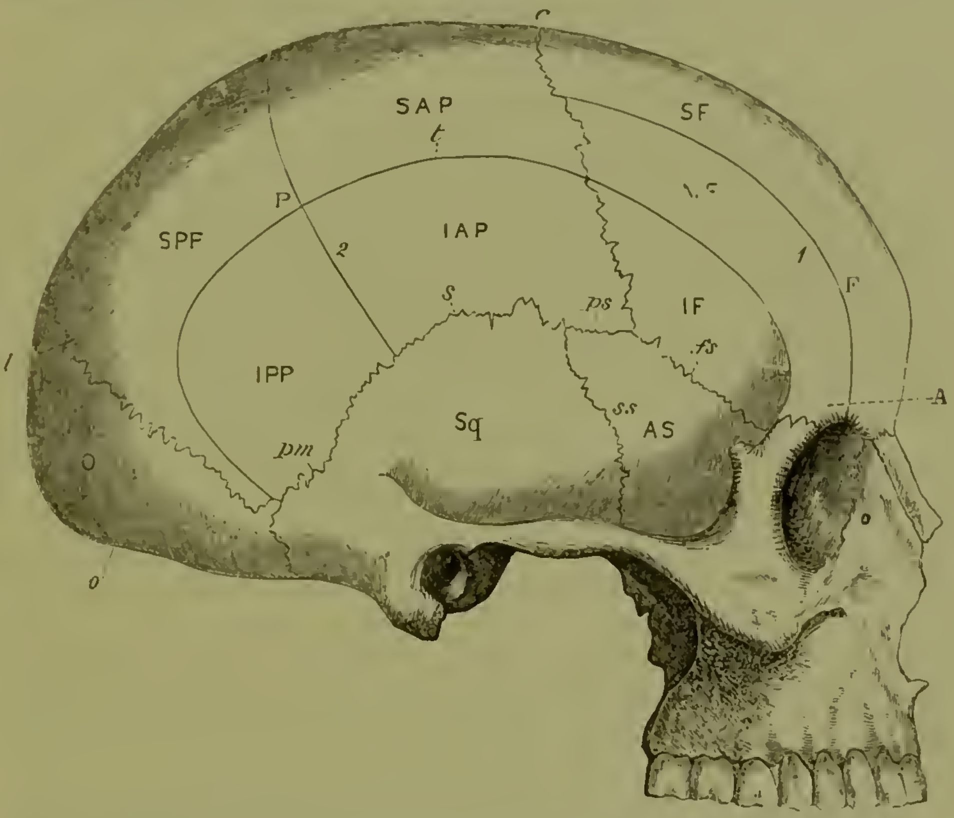

FIG. 67.—Lateral View of the Human Skull. A. The external angular process of the frontal bone. F. The frontal eminence. P. The parietal eminence. *o*. The occipital protuberance. *c*. The coronal suture. *l*. The lambdoidal suture. *s*. The squamous suture. *t*. The temporal ridge. *fs*. The fronto-sphenoid suture. *ps*. The parieto-sphenoid suture. *ss*. The squamoso-sphenoid suture. *pm*. The parieto-mastoid suture. 1. Frontal line. 2. Parietal line. SF, MF, IF. The supero-, mid- and infero-frontal subdivisions of the frontal area. SAP. The supero-antero-parietal area. IAP. The infero-antero-parietal area. SPP. The supero-postero-parietal area. IPP. The infero-postero-parietal area. O. The occipital area. Sq. The squamoso-temporal area. AS. The ali-sphenoid area.

The occipital region which lies between the lambdoidal suture (*l*) and the occipital protuberance (*o*), and the superior curved line extending on each side from it, forms the *occipital area* (fig. 67, O).

These four primary divisions are further subdivided.

The temporal ridge (fig. 67, *t*) extending backwards from the external process of the frontal bone (A), across the frontal, antero-parietal and post-parietal areas to the lateral angle of the occipital bone, divides these areas into an upper and a lower division.

We have thus an *upper* and a *lower frontal area,* S F and I F); an *upper antero-parietal* (S A P) and a *lower antero-parietal area* (I A P); an *upper postero-parietal* (S P P) and a *lower postero-parietal area* (I P P).

§ 123. The boundaries of these areas are as follows:—The *inferior frontal area*, or as it may also be called, the fronto-temporal area, is bounded above by the temporal ridge, below by the fronto-sphenoid suture, and behind by the coronal suture. The *inferior antero-parietal area* is bounded above by the temporal ridge; below by the squamous and parieto-sphenoid sutures; in front by the coronal suture, and behind by the vertical line through the parietal eminence.

The *inferior postero-parietal area* is bounded above by the temporal ridge; in front by the parietal line above referred to; below, by the posterior part of the squamous suture, and by the parieto-mastoid suture.

The upper frontal area, which includes all the frontal regions above the temporal ridge, is again divided into two, by a line drawn vertically upwards and backwards from above the orbit through the frontal eminence to the coronal suture (fig. 67, 1). This divides the upper frontal area into a *supero-frontal* (S F) and a *mid-frontal area* (M F). Hence the frontal area has three subdivisions, a supero-, infero-, and mid-frontal division.

The *upper antero-* and *postero-parietal areas* are bounded below by the temporal ridge, above by the sagittal suture, and are separated from each other by the vertical line through the parietal eminence.

Eight areas have thus been marked out. The ninth and tenth are more difficult to define, on account of this region of the skull being concealed by the temporal muscle. The areas alluded to are situated below the squamoso-parietal, sphenoido-parietal, and fronto-sphenoidal sutures.

The lines of the sutures naturally divide this region into a *squamoso-temporal* (Sq.) and an *ali-sphenoid area* (As).

§ 124. These different areas being marked off, we can now proceed to consider the relation which the fissures and convolutions have to them.

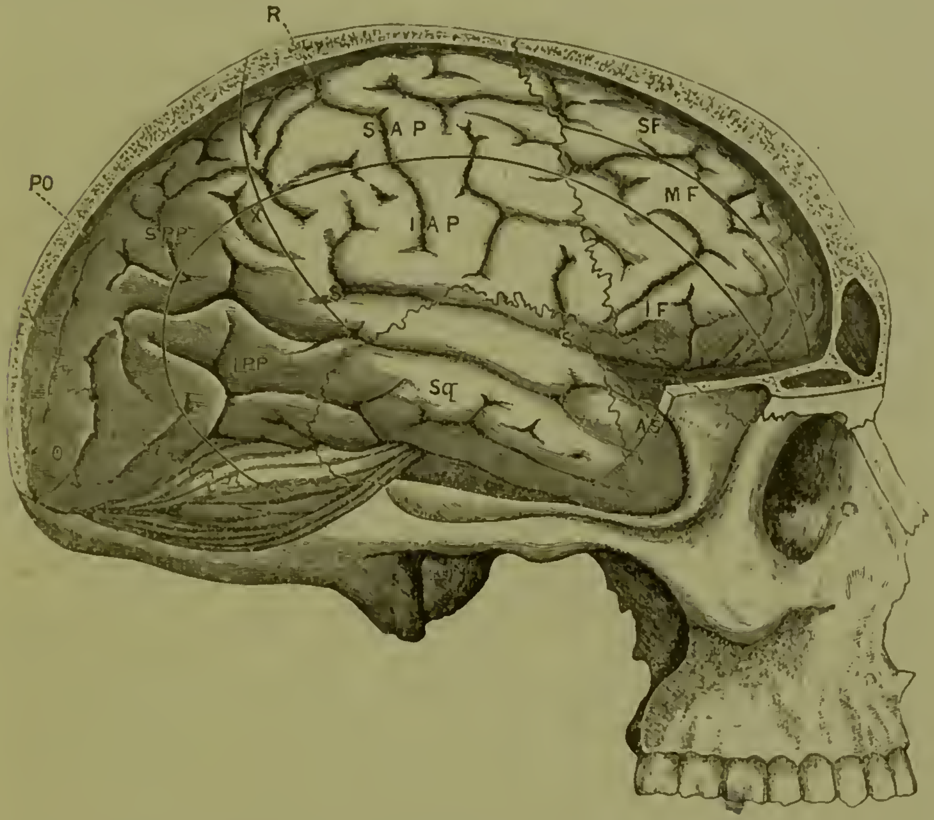

Fig. 68.—Diagram showing the Relations of the Convolutions to the Skull (Turner). R. The fissure of Rolando, which separates the frontal from the parietal lobe. PO. The parieto-occipital fissure between the parietal and occipital lobes. SS. The fissure of Sylvius, which separates the temporo-sphenoidal from the frontal and parietal lobes. SF, MF, IF. The supero-, mid- and infero-frontal subdivisions of the frontal area of the skull; the letters are placed on the superior, middle and inferior frontal convolutions. SAP. The supero-antero-parietal area of the skull: S is placed on the ascending parietal convolution, AP on the ascending frontal convolution. IAP. The infero-antero-parietal area of the skull: I is placed on the ascending parietal, AP on the ascending frontal convolution. SPP. The supero-postero-parietal area of the skull: the letters are placed on the angular convolution. IPP. The infero-postero-parietal area of the skull: the letters are placed on the mid-temporo-sphenoidal convolution. X. The convolution of the parietal eminence, or supra-marginal gyrus. O. The occipital area of the skull; the letter is placed on the mid-occipital convolution. Sq. The squamoso-temporal region of the skull: the letters are placed on the mid-temporo-sphenoidal convolution. AS. The ali-sphenoid region of the skull: the letters are placed on the tip of the supero-temporo-sphenoidal convolution.

The fissure of Sylvius (fig. 68, s) commences behind the posterior border of the lesser wing of the sphenoid, and courses upwards and backwards below the greater wing of the sphenoid, where it articulates with the anterior inferior angle of the parietal bone, and then appears in the lower part of the inferior antero-parietal region.

The fissure of Rolando (fig. 68, R) lies in the antero-parietal region, both in its superior and inferior divisions. It is situated at a variable distance behind the coronal suture, Turner finding its upper extremity sometimes as much as two inches behind the top of the suture, and its lower end as much as an inch and a half behind the lower extremity of the same. Occasionally its upper and lower extremities are not more than 1·5 and 1·3 inch posterior to the extremities of this suture respectively. It will thus be seen that the coronal suture does not correspond to the boundary between the frontal and parietal lobes of the brain, which, as has been stated, is formed by the fissure of Rolando.

The parieto-occipital fissure is situated on the average about 0·7 to 0·8 inch in advance of the apex of the lambdoidal suture (fig. 68, P O).

§ 125. Next, as regards the contents of the areas.

The *Frontal area* is entirely occupied with the frontal lobe, though it does not cover the whole of what is included under the term, inasmuch as the posterior extremities of the three longitudinal frontal convolutions, and the ascending frontal convolution, lie in the antero-parietal area. The regions included in the frontal area correspond pretty nearly to the non-excitable regions, or those which give no external response to electric stimulation. They are, according to the hypothesis advanced (Chap. XI., § 104), the motor substrata of the higher intellectual functions.

The subdivisions of the frontal area formed by the temporal ridge, and by the perpendicular drawn from the orbit through the frontal eminence, correspond to the situation of the superior frontal (S F), mid-frontal (M F), and inferior frontal (I F) convolutions.

§ 126. The *Upper Antero-Parietal Area* (S A P) contains the upper two-thirds of the ascending frontal (A P) and ascending parietal (S) convolutions, and the origins of the superior frontal and middle frontal convolutions. The former arises from the ascending frontal about 1·2 or 1·3 inch behind the coronal suture; the latter about 1 inch behind the same line. At the upper posterior angle of the area part of the postero-parietal lobule is visible, and below this, part of the supramarginal lobule may appear.

§ 127. The *Lower Antero-Parietal Area* (I A P) contains the lower third of the ascending parietal (I) and ascending frontal (A P) convolutions, and the posterior extremity of the lower frontal convolution (Broca's region). The lower frontal convolution arises from the ascending parietal, somewhat less than an inch behind the lower extremity of the coronal suture. At the upper posterior angle of this area a small portion of the supra-marginal gyrus is visible, and below this a small portion of the superior-temporo-sphenoidal convolution appears.

These two areas contain (with the exception of part of the postero-parietal lobule) all the motor centres of the limbs, facial muscles and mouth. The antero-parietal area, therefore, is more specially the motor area of the skull.

§ 128. The *Upper Postero-Parietal Area* (fig. 68, S P P) contains the greater part of the postero-parietal lobule. Below it lies the upper portion of the angular gyrus (S P P), and part of the supra-marginal gyrus (X). Posteriorly, what are generally termed the annectent gyri blend with the occipital lobe.

§ 129. The *Lower Postero-Parietal Area* (I P P) contains part of the supra-marginal gyrus, and behind it part of the angular gyrus, and below this the posterior or upper ends of the temporo-sphenoidal convolutions. The postero-parietal area taken as a whole, if we except the postero-parietal lobule, corresponds with sensory regions, and particularly with the centres of vision (the supra-marginal and angular gyri), which occupy a large extent of this area. The parietal eminence indicates the centre pretty accurately; and it might be of importance, in a phrenological sense, to determine whether there is a relation between the development of this eminence and those mental faculties of which sight is the basis.

§ 130. The *Occipital Area* (fig. 68, O) indicates the situation of the occipital lobe, though it does not entirely cover it; inasmuch as part of the occipital lobe extends anteriorly beyond the lambdoidal suture into the postero-parietal area.

§ 131. The *Squamoso-Temporal Area* (fig. 68, S *q*) contains the greater portion of the temporo-sphenoidal convolutions, but the superior-temporo-sphenoidal convolution (the centre of hearing), though for the most part under cover of the squamoso-temporal and greater wing of the sphenoid, ascends into both the lower antero- and lower postero-parietal areas.

§ 132. The *Ali-Sphenoid Area* (fig. 68, A S) contains the lower or anterior extremity of the temporo-sphenoidal lobe, and therefore corresponds to the position of the regions of smell and taste.

§ 133. The central lobe, or island of Reil, does not come to the surface, but lies concealed within the fissure of Sylvius. It is situated behind the upper part of the greater wing of the sphenoid, and opposite its line of articulation with the anterior inferior angle of the parietal bone and squamous portion of the temporal.

The convolutions situated on the internal aspect of the hemisphere are altogether out of relation to the surface of the skull.

The deep seated position and direction of the hippocampal region (the centre of touch) are superficially indicated by the convolutions of the temporo-sphenoidal lobe, contained chiefly in the inferior postero-parietal, squamoso-temporal and ali-sphenoid areas.

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